CONTRASTED CONDITIONS OF REINFORCEMENT

The effects of bidirectional changes in the incentive value of reward

Hanneke Receveur

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THE EFFECTS OF BIDIRECTIONAL CHANGES IN THE INCENTIVE VALUE OF REWARD

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PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR
IN DE SOCIALE WETENSCHAPPEN
AAN DE KATHOLIEKE UNIVERSITEIT TE NIJMEGEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS PROF DR J H G I GIESBERS
VOLGENS BESLUIT VAN HET COLLEGE VAN DEKANEN
IN HET OPENBAAR TE VERDEDIGEN
OP DONDERDAG 14 MAART 1985
DES NAMIDDAGS OM 4.00 UUR

DOOR

JOHANNA PAULA MARIA RECEVEUR

GEBOREN TE STEYL

NIJMEGEN, 1985
DRUK: DE WITTE STUDENTENPERS

Dit proefschrift is gebaseerd op projekt SW1/75 van de onderzoekspool van de Katholieke Universiteit Nijmegen.

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Chapter I

INTRODUCTION AND BACKGROUND

1.1. Theoretical points of departure

The study of behaviour of many different animal species has established quite clearly that behaviour is basically organized around the **approach** of biologically important stimuli concerning the maintenance of the subject's life on the one hand, and the **avoidance** of harmful and threatening stimuli, the protection of life, on the other hand. This classification of behaviour in biological terms is related to a distinction based on the affective value of stimuli controlling behaviour. Taken together, the stimuli involved in the above-mentioned pursuits are labelled **affective** or **incentive** stimuli. More specifically, stimuli which the animal approaches are called **appetitive** or attractive, stimuli which the animal avoids or withdraws from are called **aversive**.

Apart from determining the direction of behaviour, these stimuli also function differently in learning processes. An appetitive stimulus may function as a **reward**, through which the rewarded behaviour increases in frequency; an aversive stimulus may function as **punishment**, through which the punished behaviour decreases in frequency. In this context, both types of stimuli are labelled **reinforcers**.

Not only the stimulus' presence may influence behaviour affectively and function succesfully as reward or punishment; termination of the stimulus can do likewise. It is important to note that an animal's reaction to stimulus termination is directionally opposite to its reaction to the same stimulus' introduction. For example, a mild electroshock is an aversive stimulus which provokes avoidance or escape behaviour; shock termination causes relief reactions and must be considered comparable to an appetitive stimulus. By the same token, the effect of termination of a rewarding stimulus on learning behaviour is opposite to the effect of presentation of the same stimulus. The terms used are reward versus **frustrative nonreward** and punishment versus **relief of punishment** (Mackintosh, 1974b). See also Figure 1.1.

The importance of research into and understanding of the behavioural outcome of the interaction between aversive and appetitive stimuli, may become clear through the following considerations. First, many situations in real life are ambiguous in that they involve appetitive and aversive stimuli that are conflicted (e.g. Van der Staak, 1983). Secondly, it may increase our understanding of the functional organization of appetitive and aversive *motivational and reinforcement mechanisms*.

1.2. The nondirectional drive-theory of Hull replaced

Opinions do differ with respect to the mechanisms conceptualized to account for the interactions between appetitive and aversive stimuli in influencing behaviour's direction.

In the "General Drive"-theory of Hull (1943) which dominated the study of learning and motivation for several decades, no distinction was made between appetitive and aversive mechanisms. Directionality of behaviour was assumed to be attributable to acquired stimulus-response relationships, called habits. And drives were thought to generate behaviour, any

behaviour, indifferently. That is, the energizing effects of drive were entirely unselective and undirectional. The response with the strongest association to a given stimulus sitation would be the most likely to occur. In a later version of this theory (1952), Hull added an incentive construct K, acting in the same way as drive on habit strength to produce behaviour. Both drive and incentive motivation merely activated all response tendencies indifferently.

	APPETITIVE STIMULUS REWARD		AVERSIVE STIMULUS PUNISHMENT	
Stimulus aspects	Typical learning situation	Response probability	Typical learning situation	Response probability
PRESENTATION	approach	increases	passive avoidance	decresases
TERMINATION	time-out	decreases	escape	increases
OMISSION	extinction	decreases	active avoidance	increases

Figure 1.1. Scheme of stimulus aspects that are important for determining the direction of instrumental behaviour (Modified, after Gray, 1975). This scheme represents a simplification: in reality, these situations are often very complicated and interconnected.

Two sets of data undermined the principle of drive as an unselective energizer. First, food deprivation leads to increased activity, as predicted. However,it alters the kind of activity the animal engages in, rather than just increasing it. There is little reason to doubt that the higher activity is directed towards obtaining food: it does not represent the energizing of "any" pattern of behaviour. Secondly, a habit learned with, say, food deprivation and food reward should be energized by thirst, and even by fear. There is ample evidence that nothing of the sort does happen. Studies exploring summation of different drives and substitution of one drive by another have unequivocally shown that drives are not directionally neutral.

Hull's theory and arguments against his assumptions have been profusely reviewed (Hinde, 1970; Mackintosh, 1974b; Bolles, 1975a, 1975b; Bindra, 1976; Beck, 1978).

Though Hull's assumptions generated a vast amount of research, it has become increasingly clear, that it is important to distinguish between appetitive and aversive reinforcers/stimuli and appetitive and aversive motivational systems and to recognize that these systems interfere with each other.

Most contemporary theories of motivation and learning maintain that the motivational properties of stimuli are processed by two separate central systems or states (Mowrer, 1960; Glickman and Schiff, 1967; Berlyne, 1967, 1969; Wagner and Rescorla, 1972; Bindra, 1974; Mackintosh, 1974b;

Solomon and Corbit, 1974; Dickinson and Dearing, 1979). One system is assumed to control appetitive behaviour, and the other aversive behaviour. The dual nature of an organism's commerce with its environment is reflected in modern motivational theories, on the level of the concepts used as well as on the level of postulated mechanisms and even of underlying neural structures (Bindra, 1976).
The various incentive stimuli in conjunction with the appropriate motivational states are thought to generate either appetitive or aversive reactions, that is, either approach or avoidance behaviour. It is generally maintained that the strength of appetitive and aversive behaviour is determined by the relative level of activity in both systems. Based on a large body of experimental data (see for instance Mackintosh, 1974b), it is often argued that the operation of these systems cannot be considered independent. The operation of these systems is thought to involve an antagonistic influence on each other.
From this point of view, the idea that onset of a stimulus and termination of the same stimulus elicit responses with opposite affective directions, becomes more meaningful, as does the suggestion that a reward is functionally equivalent to relief of punishment, and punishment is equivalent to nonreward (e.g. Wagner, 1969; Rosellini, 1974; Rosellini and Terris, 1975).
There is a general agreement in the notion that the postulated motivational systems are opposite to each other and do oppose each other as well; however, the various accounts differ considerably in detail, particularly with respect to the supposed nature of the appetitive-aversive interactions.

1.3. Opponent-process theories. 1. Inhibitory interactions

A large class of theories suggests that appetitive-aversive interactions are of an inhibitory nature. When one system is activated directly, the opposite system's activity is inhibited indirectly (Mowrer, 1960; Berlyne, 1967, 1969; Estes, 1969; Wagner and Rescorla, 1972; Bindra, 1974; Gray, 1975).
Since the relative level of activity in the opponent systems determines the behavioural outcome, an additional assumption of above-mentioned theories is -if put into classical conditioning terms- that an appetitive excitor (CS+) for one system is equivalent to an aversive inhibitor (CS-) for the other, an inhibitor being a stimulus that is related to the termination or absence of the US (see Figure 1.2). Stated differently, in instrumental conditioning terms, punishment and omission of reward are viewed as more than conceptually similar: they both activate the same system; reward and relief of punishment are appreciated likewise. Generally, then, an increase in appetitive stimulation and a decrease in aversive stimulation are considered equivalent, and this also holds for the reversed case (Rescorla and Solomon, 1967; Wagner, 1969; Wagner and Rescorla, 1972; Daly, 1974a; Mackintosh, 1974b; Dickinson, 1976, 1977; Rescorla, 1977; Beck, 1978).

Since Rescorla and Solomon (1967) suggested the functional similarity of excitors and inhibitors of opposite affective values, evidence for this point of view is derived mainly from studies concentrating on the relationship between appetitive and aversive response tendencies in Pavlovian conditioning paradigms. Dickinson and coworkers have tried to

unravel the mutual antagonism of these response systems in a series of studies and developed the model depicted in Figure 1.2. As further elaboration of the tests used would take us too far afield, the reader is referred to Dickinson and Dearing (1979) for a description thereof.

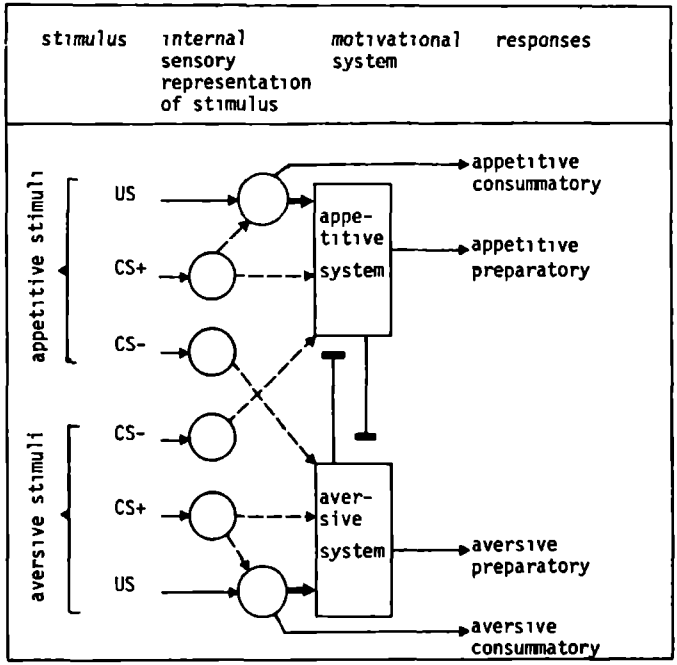


Figure 1.2. Illustration of the opponent- process model of Dickinson c.s. (modified, after Dickinson and Dearing, 1979). US: unconditioned stimulus (excitor); CS+: conditioned excitor; CS-: conditioned inhibitor; ——►: preestablished excitatory connection; ——┫: preestablished inhibitory connection; - - -►: excitatory connection established by conditioning.

From their studies and a review of the literature they conclude the following (Dickinson and Dearing, 1979):

1. On the basis of the standard summation and retardation tests, an excitor appears to have an inhibitory effect on processes controlled by an excitor of opposite affective value. According to Rescorla (1969) a stimulus must pass both the summation and retardation tests in order to be regarded as a true inhibitor of the opposite system. Although aversive stimuli have been demonstrated to have inhibitory effects on appetitive behaviour in these tests, the evidence that appetitive stimuli inhibit aversively motivated behaviour is less consistent

(Dickinson, 1976, 1977;see also Dickinson and Pearce, 1977).

2. The superconditioning effect and successful counterconditioning of the reinforcing properties of a stimulus suggest that this interaction occurs between systems mediating the motivating aspects of stimuli.
3. The interaction between an excitor of one class and an inhibitor of the opposite class must be considered as excitatory in nature, in that an inhibitor functions like an explicit excitor of the opposite value, modulating reinforcement and extinction processes controlled by the excitor. This was revealed by blocking and extinction tests. Although it appears that an appetitive inhibitor can modulate aversive conditioning and extinction in a manner that parallels an explicit aversive excitor, there is little evidence for the reverse, namely an effect of an aversive inhibitor on processes controlled by an appetitive excitor.

Discussing these data in detail is beyond the scope of our study. The general results of these types of experiments have been reviewed by Dickinson and Dearing (1979) and Dickinson and Pearce (1977).

Another set of data may be considered support for the inhibitory nature of aversive-appetitive interactions. These are the demonstrations of behavioural contrast effects, particularly those of the transient or local variety (see Chapter 2.3.3).

Whereas Dickinson c.s. concentrate on the direct effects of the various stimuli and do not explicitly deal with the after-effects of these stimuli, related theories do. These theories, developed around the concept of conditioned inhibition suggest that removal of an inhibitor will result in disinhibition or rebound, as is apparent in the temporarily enhanced responding, called positive induction by Pavlov in "Lecture 11" (1927/1960) or positive behavioural contrast effect in more recent research (D.R. Williams, 1965; Nevin and Shettleworth, 1966; Brimer, 1972; Mackintosh, 1974b). Generally, a Pavlovian orientation has been taken.

The rebound argument, then, runs as follows. Omission of, say, an appetitive reinforcer or presentation of a stimulus signalling such omission (CS-) inhibits the appetitive central motivational system. Though the CS- signals absence of reinforcement, it is also highly correlated with an eventual presentation of reinforcement, due to its conditioning to situational cues, and thus it acquires excitatory properties. On the other hand, CS- is a negative stimulus with regard to the immediate presence of the reinforcing event and therefore acquires inhibitory properties. For a CS- to effectively function, its inhibitory strength must be greater than its excitatory strength (D.R.Williams, 1965; Nevin and Shettleworth, 1966; Rescorla, 1969; Wagner and Rescorla, 1972; Mackintosh, 1974b). Removal of this CS- will release the central motivational system from the inhibitory influence. Therefore, the activity of this system will rebound to a level temporarily above normal, due to the excitation built up also during the CS-. Along the same lines, removal of a CS+ may release the central motivational system from excitatory influences and therefore cause a decrease in the system's activity temporarily below normal. It is precisely the symmetry observed in local contrast phenomena that, according to Mackintosh (1974b), strongly suggests a rebound interpretation.

Data concerning local contrast and other contrast effects will be considered in detail in Chapter II.

1.4. Opponent-process theories. 2. Excitatory interactions

Dickinson c.s. varied the affective value of the eliciting stimulus and emphasized behavioural interactions between aversive and appetitive stimuli. Thus, they focused their attention mainly on behavioural changes during presentation of the stimuli and derived inhibitory relationships between the opposite affective systems from the testresults. Diametrically opposed to the inhibitory interaction models is the theory proposed by Solomon and Corbit (1974), who compare behavioural effects following onset and offset respectively of affective stimuli. This different approach led them to develop an excitatory interaction model.

The major concern of this opponent-process theory has been to account for the phenomenon of affective contrast, and the tolerance and withdrawal syndrome seen in addiction. The term "affective contrast" refers to "the fact that the sudden removal of a reinforcer can induce an affective state quite unlike that induced by the presence of the reinforcer" (Solomon, 1982). Indeed, this state appears to have an opposite affective value. The withdrawal syndrome appears only after habituation or tolerance to the reinforcing stimulus has developed; it is characterized by the intensification of affective reactions whenever the reinforcer is terminated or omitted (Solomon and Corbit, 1973). It is important to note that the affective reaction to the presence of the stimulus event declines with repetition (habituation, tolerance), whereas the contrasting after-reaction intensifies with repetition.

The model devised by Solomon and Corbit (1974) to account for these phenomena can be summarized as follows:

1. The onset and maintenance of a reinforcing stimulus sets into action a primary affective process, called the a-process. It is quick and tracks the stimulus intensity and duration quite accurately; it collapses with termination of the stimulus. This a-process, in turn, generates and maintains a certain affective state (state A), pleasant or unpleasant, which constitutes a deviation from the affective equilibrium.
2. Arousal of the a-process eventually will lead to the engagement of an opponent process, the b-process, which opposes state A, that is, reduces its affective intensity.

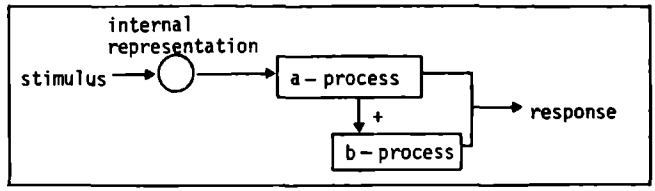


Figure 1.3. Illustration of the opponent-process theory according to Solomon and Corbit (1974).

The b-process is conceived as a slave-process: it can not be aroused directly by ordinary stimulation input, but instead can be aroused only indirectly via the arousal of the a-process (Figure 1.3). Unlike the a-process, the b-process is postulated to be sluggish in its latency, its recruitment and decay, relative to the a-process.

3. The output of the two opponent systems is algebraically summed and the resultant manifest affective state is determined at any given moment (Figure 1.5, panel I). Because of the lower asymptote of the b-process, we cannot observe its affective quality as long as the arousing stimulus is present. The b-process is active, though, and minimizes deviations from the affective equilibrium, producing what is called adaptation (Hoffman and Solomon, 1974). However, with the cessation of the significant stimulus, the b-process manifests itself. The a-process dies out quickly, but the b-process, following the events more sluggishly, is still active; therefore, the A-state does not simply collapse into neutrality, but, rather, it swings beyond and into the opposite (state B). It then slowly returns to neutrality. Thus, neutrality can only be achieved biphasically (Figure 1.4).

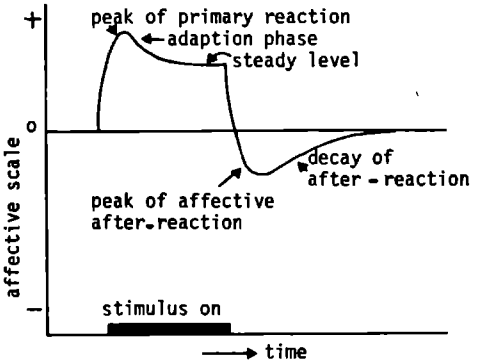


Figure 1.4. The standard pattern of affective dynamics (Solomon and Corbit, 1974).

4. With repeated exposure to the stimulus, both manifest states (A and B) change: as habituation progresses, state A declines, but the after-effects do not become smaller; instead they become larger (state B increases). An additional postulate is that these changes reflect underlying changes in the b-process. It is assumed that the b-process will be strengthened by use and weakened by disuse (Figure 1.5, panel II), whereas the a-process remains essentially unchanged. Both habituation and the withdrawal syndrome are thus brought about by the b-process.

This opponent-process theory of affective dynamics clearly mirrors physiological theories for sensory or neural organization (e.g. Hurvich and Jameson, 1974).

At the time of its initial development, little empirical evidence existed in support of the theory, apart from anecdotal data (Solomon and Corbit, 1973, 1974) and post hoc analyses of earlier experiments not specifically designed to test the theory (Rescorla and Lolordo, 1965; Church et al., 1966; Moscovitch and Lolordo, 1968; Katcher et al., 1969; Solomon and Corbit, 1974). At the moment, however, evidence from the animal laboratory is accumulating and covers areas as diverse as imprinting (Hoffman and

Solomon, 1974; Starr, 1978), fear conditioning (La Barbera and Caul, 1976a, 1976b), schedule-induced polydipsia (Rosellini and Lashley, 1982), tonic immobility reactions (Berns and Bell, 1979). Experimental evidence from the area of human behaviour is growing as well (e.g. Solomon and Corbit, 1973; Solomon, 1977a; Craig and Siegel, 1979; Solomon, 1980, 1982). Experiments pertaining to this opponent-process theory have been recently reviewed by Solomon (1980).

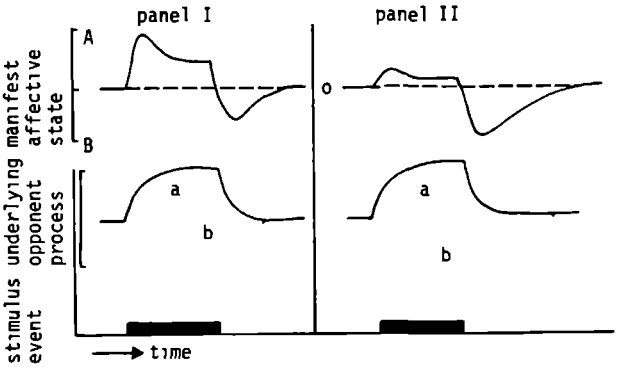


Figure 1.5. The standard pattern of affective dynamics(1.5, panel I). The change in the manifest affective state (1.5, panel II) is brought about by the increase in the strength of the b-process through repetition (after Solomon, 1980).

One feature of this opponent-process theory which distinguishes it from the foregoing inhibitory model, is the fact that in the present model both opponent affective systems are engaged by one and the same stimulus, one system directly and the other indirectly, whereas in Dickinson's model the opponent processes are activated only by stimuli of contrasted affective value (Figure 1.3).

More important is the differing account of the after-effects of affective stimulation. Though Dickinson's model does not explicitly deal with those effects, related inhibitory models assume the after-effects to result from a release of inhibition or rebound. This rebound does not occur, of course, if there was no inhibition involved, and if it does, its size is proportional to the size of the primary reaction and becomes smaller as the primary reaction decreases through habituation (D.R.Williams, 1965; Mackintosh, 1974b). In contrast, Solomon and Corbit (1974) suggest that the after-effect is always present; initially it may be small in proportion to the primary reaction, but it becomes larger as habituation proceeds, whereas, at the same time, the primary effect diminishes (Hoffman and Solomon, 1974).

Chapter II

CONTRAST EFFECTS

2.1. The issue of symmetry and contrast phenomena

As will be clear from the preceding chapter symmetry is a central feature in both excitatory and inhibitory theories of affective dynamics. Whether their nature is excitatory or inhibitory, interactions between appetitive and aversive systems are assumed to be symmetrical in both cases.
One type of situation which seems preeminently suited to examine, first of all, this theoretical symmetry and, secondly, potential changes in reactions through use, is the contrast experiment. The term contrast was proposed in analogy to the contrast phenomena described in connection with the physiology of the sense organs. In the psychology of learning and motivation the term contrast refers to behaviour which indicates that "the influence of a given reward event is exaggerated by the nature of other reward events to which the animal is exposed" (Rashotte, 1979b).
A vast amount of literature documents various types of contrast effects. One of the main contrast paradigms has been developed explicitly to refute Hull's theory of general drive (Crespi, 1942). The contrast research received a second impulse through theories of conditioned inhibition, and contrast phenomena were considered the "most dramatic demonstrations" of the interactions of opposed motivational processes (D.R.Williams, 1965). Even though these experiments have been important stimulants for theoretical development, the main body of the literature concerning contrasts has not adressed itself directly to the topic of affective dynamics and models of interaction therein, but has preferred either more modest models accounting for only limited sets of data, or has concentrated on purely associative models of operant conditioning. Thus, procedures and theoretical frameworks employed in these studies have tended to keep them isolated from general theories that explicitly deal with the motivational dynamics that underly behaviour. Nevertheless, contrast effects seem distinctly relevant to the general subject.
First, the study of contrast effects is, in fact, concerned with the effects of **transitions** between different reinforcing events or stimuli correlated with different reinforcing events. Attention is focused not only on the effects of presentation of these reinforcing events and stimuli, but on the effects of termination as well, perhaps even more so **(after-effects)**.
Secondly, the issue of **symmetry** of the effects is as important for models explaining contrast effects alone, as it is for the more general motivational opponent-process theories.
And finally, because contrast paradigms typically contain **repeated** presentations of changes in the reinforcing events, potential changes in reactions through use will be revealed.
In most contrast paradigms reinforcement changes, called **shifts**, are superimposed on operant tasks that maintain a stable level of responding over time, e.g. barpressing or running through an alley. The deviations from this stable response level are thought to reflect the effects of the reinforcement shifts. For example, a rat has been trained to perform a barpress response at a certain rate (the base level); next, a temporary (and signalled) change in the reinforcer is introduced, followed by a return to the original reinforcer. If, after a shift in an unfavourable

direction, the original reinforcer has gained a higher value than before the shift, as indicated by an increased response level, a **positive contrast effect** is said to occur. The reverse case, a shift in a more favourable direction, may produce a **negative contrast effect.**

Before reviewing the present state of affairs in the research pertaining to contrast effects, a few terms will be clarified.

2.2. A typology of contrast effects. Definition of terms

Rewards may vary along a number of dimensions, the most important of which are: quantity (number of pellets, volume of liquid, duration of reward presentation), quality (concentration of solution, taste, preferred versus nonpreferred reward), probability (frequency, partial reinforcement, nonreward/omission) and delay of presentation. Changes along these dimensions appear to alter the reward "value", as is revealed by the animal's altering performance after manipulation of the reward values.
When an animal is confronted with a reward of a particular value after experience with a reward of a different value, its performance for that reward, or for both, will be changed. If confronted with a large reward value after experience with a smaller one, the animal may respond more vigorously for this large reward then if it were confronted with the large reward all along. By the same token, a decreased performance may be produced by a smaller reward value after experience with a larger one.
Both behavioural changes are termed contrast effects, **positive contrast effects** (PCE) and **negative contrast effects** (NCE) respectively. The term contrast, borrowed from perceptual physiology, is used to describe any exaggerated responding for one reward value, due to it being presented in close temporal proximity with another reward value (Flaherty, 1982).
If, on the other hand, performance for one reward value changes in the direction of the performance for the other reward value, **induction** is said to occur. Thus, if performance for a large reward value -due to it being presented in the context of a small reward value- is less than if the larger reward was given all along, the effect is called a **negative induction effect** (NIE). Its pendant is the **positive induction effect** (PIE).
The terms contrast, induction, positive and negative tell something about the direction of the behavioural changes. Apart from this aspect, a variety of contrast phenomena may be distinguished. Though it is often difficult to compare the various studies concerned with contrast effects, due to their vastly diverging procedures, a main division of the effects might be based on the temporal aspects of the presentation of reward changes and associated stimuli (shifts).

1. **Successive contrast effects**, then, are studied in experiments in which subjects are initially trained on one reward, and are subsequently shifted to a different reward in the same task; the different reward values are presented successively (Crespi, 1942).
2. **Simultaneous contrast effects**, on the other hand, occur in situations in which subjects receive different reward conditions in some intermixed order during a single training session (Bower,1961). Though both rewards are not offered simultaneously in the true sense, the term stresses the importance of close temporal proximity of the different rewards as well as the repetition of shifts. Actually, the simultaneous contrast paradigm is a differential conditioning procedure, a special

stimulus being used to signal which reward condition is in effect. Both the successive and the simultaneous contrast effects are designated **incentive contrast effects** (Cox, 1975; Flaherty, 1982). Important aspect of incentive contrast studies is that the changed incentive value of rewards -as reflected in the animals' changed performance- is evaluated against the performance of a non-shifted reference group (between-Ss design).

3. However, each subject's own baseline performance prior to changes in reinforcement conditions, can also be taken as the control value against which to judge changes in performance. This within-Ss design is a basic feature of a third group of contrast experiments studying **behavioural contrast effects**. The term behavioural refers to the measurement of differences in behaviour within one-and-the-same subject (Reynolds, 1961a, 1961b). Usually, free operant tasks are employed. In a sense, behavioural contrast paradigms might be considered a special case of simultaneous contrast procedures (Mackintosh, 1974b), because here too different reward values are presented intermittently and they are cued. But there are many differences as well. The similarities and dissimilarities will be considered in detail in section 2.4.3 of this chapter .
4. Finally, in some behavioural contrast paradigms contrast effects are also evident in very localized portions of the several reward conditions, particularly in the periods immediately after the transition from one condition to the other. These effects are called **transient contrast effects** by some (e.g. Mackintosh, 1974b), though they are often not transient at all, or **local contrast effects** by others (Nevin and Shettleworth, 1966; Rashotte, 1979b; Williams, 1983).
These, then, are the phenomena one may encounter when diving into the overwhelming multiplicity of the research focusing on contrast effects. There is by no means agreement as to the terminology applied to the various contrast paradigms and contrast phenomena. Nevertheless, the outlines as presented above are generally accepted.

As can be deduced from the foregoing, most contrast research has concentrated on changes in appetitive reinforcers; studies employing aversive reinforcers are very few (Bower et al., 1959; Wertheim, 1965; Woods, 1967; Bertsch and Leitenberg, 1970; Bintz, 1971; Shanab and White, 1972; McAllister et al., 1972; Rosellini, 1974; Nation et al., 1974; Nation et al., 1975; Rosellini and Terris, 1975; Roop and Nation, 1976).

Appetitive and aversive reinforcers can both be changed for the better as well as for the worse. Thus, changes into both directions can be effectuated and their behavioural effects measured. Also, a given stimulus may produce either positive or negative contrast during a series of stimulus presentations. The contrast effect that occurs, is determined by its value in relation to the alternative stimuli, not by some absolute classification of whether the stimuli are appetitive or aversive, and whether they are excitatory or inhibitory.

2.3. Current state of affairs in the contrast research: major empirical findings

In this section each of the main categories of contrast effects will be treated separately and the major empirical data will be considered. Research on contrast phenomena has become so massive that an exhaustive

review would be too large an undertaking. Moreover, studies pertinent to incentive contrast effects of both classes have recently been reviewed by Mackintosh (1974b), Cox (1975), Flaherty (1982); and studies using behavioural contrast procedure have been considered by Mackintosh (1974a), McSweeney et al. (1981) and Williams (1983). Therefore, it would be repetitious to present the relevant research here in detail. Instead, it is intended to report only main trends in the experimental data. Readers are referred to above-mentioned articles for more detailed surveys. First, successive contrast effects will be presented (2.3.1), followed by simultaneous contrast effects (2.3.2), and finally behavioural plus local contrast effects (2.3.3).

2.3.1. Successive contrast effects

The basic scheme of a successive contrast paradigm is given in Table 2.1. Animals are trained to run in an alley for reward value X, are then shifted to reward value Y in the same alley, and their change of performance is evaluated against the performance of a group having received reward value Y all along. The great majority of the research into successive contrast effects has employed rats for subjects and was conducted in alleyways, using running times or speed as measures of performance. The first systematic study of successive contrast effects (Crespi, 1942) demonstrated both negative and positive contrast effects, called depression and elation respectively by Crespi. Together with the undershooting and overshooting of control levels of performance, it was the abruptness of the performance changes that forced Hull to revise his theory. Crespi's results suggested that variations in reinforcement did not affect learning (Hull's habit: H) but did affect performance instead. Hull then reformulated his postulate that behaviour is determined entirely by drive (D) and learning or habit strength (H), and added the construct of incentive motivation (K) to the behaviour equation, so that Behaviour = K x D x H. Thereafter, much research was devoted to the phenomena revealed by Crespi. But while the negative contrast effect was readily demonstrated under a variety of test conditions, the positive contrast effect proved more elusive. Consequently, Crespi's positive contrast effect has been attributed to procedural artefacts and the successive positive contrast effect has been considered nonexistent (Black, 1968; Dunham, 1968; Campbell et al., 1970). However, it may well be that procedural artefacts, e.g. ceiling effects, obscure rather than produce the occurrence of positive contrast effects. If, for example, reinforcement is delayed to produce an overall slower running, rats do show a positive contrast effect (Schrier, 1967; Shanab et al., 1969; Mellgren, 1971a, 1971b, 1972; Shanab and Biller, 1972; Mellgren et al., 1972; Shanab and Cavallaro, 1973; Shanab and Spencer, 1978; Spencer and Shanab, 1979; see also Flaherty, 1982). Generally, it seems that the positive contrast effect more readily occurs if subjects have been submitted to a downward shift that is significantly frustrative, prior to being upshifted again (Harris et al., 1962; Spear and Spitzner, 1968; Benefield et al., 1974; McCain and Cooney, 1975; Maxwell et al., 1976; Rashotte, 1979b).
Reinforcement value may be varied along several dimensions. In successive contrast studies, however, more often than not quantity of solid food reward was varied to induce the performance changes under study. With changes in quantity of reinforcement, then, the negative contrast effect is consistently produced, whereas positive contrast effect is somewhat less

reliably obtained; nevertheless, contrary to what is maintained in prior reviews (Black, 1968; Dunham, 1968) the positive contrast effect can be obtained (Ehrenfreund and Badia, 1962; Spear and Hill, 1965; Seybert and Mellgren, 1972;Mellgren et al., 1973; Benefield et al., 1974). Both the negative and positive contrast effect are, in a sense, transient effects; that is, they disappear after a number of trials.

Table 2.1. Schematic representation of basic designs typically employed in the main varieties of contrast studies. Given are groups of subjects commonly employed and (imaginary) reward values each group receives per phase of the experiment, either in one unchanged situation (as is the case in the successive contrast experiment) or in a differential-conditioning situation (as in the case in the others) with S1 signalling one value of reward and S2 signalling another value. The same scheme can be drawn for paradigms researching negative contrast effects.

	INCENTIVE CONTRAST	DIFFERENTIAL CONDITIONING CONTRAST	
	Successive contrast	*simultaneous contrast*	*behavioural contrast*
PRESHIFT phase 1.	group (10)—10 pellets group (1)— 1 pellet	group E:S1—10; S2—10 group C:idem this phase is usually not present	S1—VI-30; S2--VI-30
TEST phase 2.	group (10)—10 pellets group (1)—10 pellets	group E:S1—10; S2— 1 group C:S1—10; S2—10	S1—VI-30; S2--EXT
COMPARE	between subjects	between subjects	within subjects
PCE occurs	if in phase 2 group (1) > group (10)	if in phase 2 group E > group C in responding for S1	if responding for S1 in phase 2 > phase 1

Initially, no contrast effects were found with changes in quality of reward (Goodrich and Zaretsky, 1962; Homzie and Ross, 1962; Hulse, 1962; Spear, 1965; Rosen, 1966; DiLollo and Meyer, 1970; Barnes and Tombaugh, 1973). Quality is most often varied by offering different concentrations of sucrose solution. If, however, instead of speed, consummatory responses (lick rates) or lever press responses were measured, both negative and positive contrast effects were obtained (Collier and Marx, 1959; Collier et al., 1961; Rosen and Ison, 1965; Vogel et al., 1968; Gandelman and Trowill, 1969; Weinstein, 1970a, 1970b; Ashton and Trowill, 1970; Ashton et al., 1970; Dube et al., 1970; Panksepp and Trowill, 1971; Weinstock, 1971; Flaherty and Hamilton, 1971; Likely et al., 1971; Weinstein, 1972a; Flaherty et al., 1973b; Shanab et al., 1975a, 1975b; Burns, 1976; Flaherty and Caprio, 1976; Ciszewski and Flaherty, 1977; Burns and Burns, 1978; Burns et al, 1978; Weinstein, 1978a, 1978b; Lombardi, 1979; Boyer and Swank, 1980). These contrast effects do differ from the effects found

after changes in quantity of reward with speed measures: they develop more slowly and they are quite persistent (Bolles, 1975a; Flaherty, 1982).
Shifts in schedules of reward (probability) readily produce successive contrast effects, both negative and positive (Leung and Jensen, 1968; Fox, 1972; Calef et al., 1973; Lehr, 1974; Shanab et al., 1974; Shanab and Cavallaro, 1975, McHose and Peters, 1975; McCain et al. 1976b; Dijck et al., 1977; McHose and Moore, 1978; Seybert, 1979). In contrast, shifts in delay of reward produce neither a negative nor a positive contrast effect (Harker, 1956; Logan, 1960; Shanab, 1971; Shanab et al., 1973; Cox and Black, 1975; Ferrell and Shanab, 1975; McCain et al., 1977; Flaherty, 1982).
Test factors which may enhance successive contrast effects are: increase in disparity of the reward values used, increase in number of preshift training trials, the use of massed instead of spaced trials, increase in the level of deprivation (Crespi, 1944; Gonzalez et al., 1962; DiLollo and Beez, 1966; Vogel et al, 1966; Dunham, 1967; Cleland et al., 1969; Gonzalez and Bitterman, 1969; Shanab and Ferrell, 1970; E.D.Capaldi, 1971; Ehrenfreund, 1971; Calef, 1972; E.D.Capaldi and Singh, 1973; Flaherty and Kelly; 1973; Peters and McHose, 1974; Forster, 1976; Oscos Alvarado, 1976; Weinstein, 1977b; E.D.Capaldi et al., 1977; Moore, 1979; Riley and Dunlap, 1979). Training on a partial reinforcement schedule and a long training-test interval weaken contrast effects (Gleitman and Steinman, 1964; Mikulka et al., 1967; Gordon et al., 1973; Ciszewski and Flaherty, 1977).
Taking all evidence together, it is clear that the negative contrast effect is an effect easily obtained, as long as amount of reward is varied, and that there is also substantial evidence for the positive contrast effect. However, special steps have to be taken to demonstrate the positive contrast effect which, at the very least, suggests that the positive contrast effect is not entirely equal to the opposite negative contrast effect.
These conclusions only pertain to rats. One very important aspect seems to be the animal species chosen to study the topic. As it is, neither pigeons nor turtles have ever shown positive or negative contrast effects (Gonzalez et al., 1967; Lowes and Bitterman, 1967; Pert and Bitterman, 1970; Gonzalez et al., 1972; Wolach et al., 1973; Cochrane et al., 1973; Wolach and Latta, 1974; Bitterman and Schoel, 1970; Bitterman, 1975; Bitterman et al., 1979). In fish the evidence is ambiguous (Raymond et al., 1972; Gonzalez et al., 1974; Breuning, 1978; Breuning et al., 1977, 1980). Successive contrast effects have also been reported with humans (Weinstein, 1970c, 1981, 1982).

2.3.2. Simultaneous contrast effects

As indicated in Table 2.1, in a simultaneous contrast procedure subjects are concurrently exposed on random alternating trials to one condition of reinforcement, X, in one stimulus situation, and a different condition of reinforcement, Y, in a second stimulus situation. Changes in behaviour are evaluated against the performance of the appropriate nonshifted control groups; that is, groups receiving either one, X, or the other, Y, reward value for responding in the presence of both stimuli.
As both stimulus alternatives are not available at the same time, the term simultaneous contrast is deceiving. The paradigm is in fact a successive differential conditioning procedure, in which stimuli and associated reward

values are repeatedly shifted during a single session. The nondifferential training phase, mentioned in table 2.1, is usually but not always absent. Rats are the most commonly employed subjects. Almost always the procedure involves discrete trials, uses alleys (e.g. one black, the other white), and measures running times or speed.

Since the classic study of Bower (1961) the general pattern of results has not undergone many changes. Bower had rats running for a large reward in one alley and for a small reward in a second alley. They ran more slowly for the small reward than a small-reward control group did, thus showing a negative contrast effect. There was no evidence for a comparable positive contrast effect. Bower attributed the absence of the positive contrast effect to ceiling effects: if performance of control groups was at an upper physiological limit, demonstration of a positive contrast effect was prohibited. As mentioned before, the same argument was used to explain the absence of successive positive contrast effect with locomotor responses.

The simultaneous negative contrast effect is a far more general phenomenon than is the successive negative contrast effect. It is demonstrated under a considerable range of conditions: shifts in quantity, quality or delay of reward all produce the depressed responding relative to control group's performance (Logan, 1952; Bower, 1961, 1962; Ludvigson and Gay, 1966; Rossman and Homzie, 1967; Beery, 1968; Matsumoto, 1969; Gavelek and McHose, 1970; Shanab and McCuiston, 1970; McHose and Tauber, 1972; Mackintosh and Lord, 1973; Chechile and Fowler, 1973; Flaherty et al., 1973a; Calef et al., 1975; Flaherty and Avdzej, 1976; Flaherty et al., 1977; Flaherty et al., 1982).

Variations in reward percentage have not produced evidence for simultaneous negative contrast effects (Henderson, 1966; Spear and Pavlik, 1966; Galbraith et al., 1968).

Generally, the negative contrast effects develop slowly as discrimination learning proceeds, and once developed they persist for a long time, if exposure to the other reward value is continued.

As was the case with successive contrasts, the simultaneous negative contrast effect increases with greater difference between the reward values used. Also, the shorter the intertrial interval, the clearer is the contrast (McHewitt et al., 1969; Krane and Ison, 1970, 1971; Haggbloom, 1979; Flaherty, 1982). Contrary to the successive contrast effects, type of response measured seems largely irrelevant: the negative contrast effect has been found with locomotor responses, latency measures, intake measures, lick rate, leverpress responses and keypeck responses (Flaherty et al., 1973a; Gonzalez and Champlin, 1974; Flaherty and Avdzej, 1974; Flaherty and Largen, 1975; Flaherty and Lombardi, 1977; Lombardi and Flaherty, 1978; Flaherty et al., 1979b).

The simultaneous negative contrast effect has also much larger generality than the successive negative contrast effect from a comparative point of view. Simultaneous negative contrast effects have been reported in fish, turtles, pigeons, monkeys and humans (Schrier, 1958, 1962, 1965; Brownlee and Bitterman, 1968; Calef et al., 1971; Cochrane et al., 1973; Gonzalez and Powers, 1973; Burns et al., 1974; Pert and Gonzalez, 1974; Gonzalez and Champlin, 1974).

In comparison to the consistent findings of negative contrast effects, the evidence for simultaneous positive contrast effects is far from unanimous. Bower (1961) attributed his failure to demonstrate a positive contrast effect to ceiling effects, whereas others pointed at the long inter-trial-intervals (ITI) used in his study. Nevertheless, the majority of studies designed to detect a positive contrast effect were unable to do

so (Black, 1968; Dunham, 1968; Cox, 1975). In fact, often the opposite was found, a reliable negative induction effect, i.e. a depression in speed for a large reward , as compared with a large reward control group, induced by the small-reward alternative (Bower, 1961; McHose and Ludvigson, 1965; Peckham and Amsel 1967; Matsumoto, 1969; Gavelek and McHose, 1970; Chechile and Fowler, 1973; McHewitt, 1974; Calef et al., 1975; Shanab and Kong, 1977).
If, however, certain steps are taken, for example, if delays are introduced, very short ITI's are used or if the predictability of the reward value to be expected, is increased, positive contrast effects are sometimes found (Daly, 1968; Mellgren et al., 1972; Mellgren and Dyck, 1974; Flaherty and Largen, 1975; Calef et al., 1975). It is often suggested that latency measures are simply not sensitive to positive contrast effects (e.g. Mackintosh, 1974a, 1974b; Rashotte, 1979b); first, the already mentioned ceiling effects might prevent a positive contrast effect to be detected; and secondly, latency measures may reflect decision-time problems which will interfere with positive contrast effects (Daly, 1968; Mellgren et al., 1972). Presumably, there are no such problems with rate measures.
One final procedure remains to be mentioned because it consistently produces simultaneous positive contrast effects, as well as negative contrast effects: if the concentration of a sucrose solution is varied within a session, and if, more importantly, instead of instrumental responses consummatory responses, either lick rate, or intake, or latency to switch tubes, are measured, reliable positive and negative contrast effects are found, the effects being more robust in rate measures than in latency measures (Flaherty and Avdzej, 1974; Flaherty and Largen, 1975; Flaherty and Lombardi, 1977; Flaherty et al., 1977; Flaherty et al., 1979b; see also Boyer and Swank, 1980).
In conclusion, then, the simultaneous negative contrast effect has been abundantly demonstrated, but the pendant positive contrast effect is not found widely. Despite this imbalance in evidence, the positive contrast effects found do not appear to represent chance findings. The reason for this imbalance in simultaneous contrast findings are not well understood.

2.3.3. Behavioural contrast effects

Behavioural contrast studies typically employ multiple schedules. To detect contrast effects, subjects are repeatedly exposed to two stimuli in succession. During the nondifferential preshift training phase, both stimuli are associated with the same schedule of reinforcement. During the shift phase one stimulus is associated with the original schedule (the unchanged component); the second stimulus now signals another schedule of reinforcement (the variable component). Contrast is said to occur if performance in the unchanged component is influenced by the schedule in the variable component, such that it changes in a direction opposite to the performance change directly induced by the shift in reinforcement in the variable component (see Table 2.1). Thus, positive contrast occurs if performance in the unchanged component increases, due to the variable component being shifted to a less preferred reinforcement schedule. It is important to note that the performance in the unchanged component is compared with performance under the same reinforcement schedule during the nondifferential training phase; i.e. the performance of each subject is evaluated against its own previously established base level of responding:

results are considered per subject (see Figure 2.1). It has been shown that a within-Ss design shows a greater sensitivity for changes in reinforcement (McHose, 1963; Hamm, 1967; McHose and Gavelek, 1969; Mackintosh et al., 1972; Gonzalez and Champlin, 1974; Boakes et al., 1976). And whereas some consider this an advantage (Mackintosh, 1974b), others would say that the within-Ss design is "prone to overestimate the size of the contrast effects" (Rashotte, 1979b). This is, of course, two different ways of saying the same thing.
As already indicated, behavioural contrast studies generally utilize free operant procedures in which the subject is permitted to respond at its own rate. Performance is measured in terms of rate of responding over time (barpress rate, keypeck rate etc.). And much more than was the case with the other types of contrast research, pigeons have been used as subjects. In fact, for a long time, behavioural contrast effects have been considered peculiar to pigeons (Freeman, 1974; Hearst and Jenkins, 1974).
Within the context of behavioural contrast two main types of effects are often distinguished: the overall behavioural contrast effect occurring over the entire time the stimulus signalling the unchanged component is present; versus a contrast effect which is evident in more localized periods of the stimulus presentation (hence **local** contrast effect), particularly in the period immediately after transition from variable component to unchanged component (see Figure 2.1).

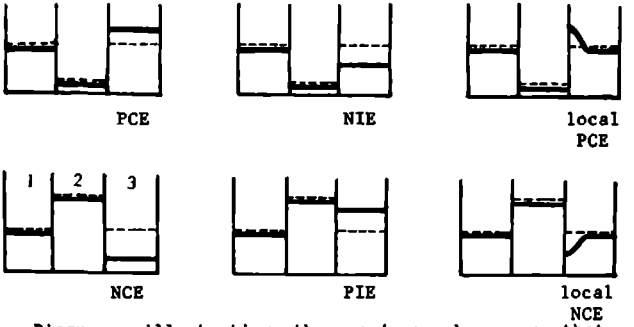


Figure 2.1. Diagrams illustrating the various phenomena that may be encountered in a behavioural contrast paradigm employing multiple schedules. Unchanged components (1 and 3) are alternated with variable components (shift: 2) in which the value of the reinforcer is altered. To evaluate the phenomena which occur in the unchanged component (3) following the shift, response rates of the components before and after the shift have to be compared. Both left-hand diagrams represent overall behavioural contrast effects, the middle diagrams depict induction effects, and the right-hand diagrams depict the local variety of contrast effects. ———: reinforcement value; ———: response rate; NCE: negative contrast effect; PCE: positive contrast effect; NIE: negative induction effect; PIE: positive induction effect. (Reprinted with kind permission of dr. P. Kop).

A negative as well as a positive contrast effect of the local contrast variety have been demonstrated in both pigeons and rats (Boneau and Axelrod, 1962; Catania and Gill, 1964; Bloomfield, 1966, 1967a, 1967b;

Nevin and Shettleworth, 1966; Terrace, 1966a, 1966b; Bernheim and Williams, 1967; Wilton and Clements, 1971; Vieth and Rilling, 1972; Mackintosh et al., 1972; Malone and Staddon, 1973; Benefield, 1974; Buck et al., 1975; Innis, 1978). Local contrast effects generally develop after a few sessions and disappear again once the component discrimination is fully mastered (Nevin and Shettleworth, 1966; Bernheim and Williams, 1967; Hearst, 1969; Knowles, 1973; Malone, 1976; MacDonall and Marcucella, 1978; Hinson and Malone, 1980; Hinson and Staddon, 1981; Williams, 1981, 1983; Blough, 1983). For this reason the local contrast effect has also been termed **transient** contrast effect; however, the term local contrast effect is preferable because sometimes the effects do not decrease at all over sessions (Catania and Gill, 1964; Staddon, 1969; Arnett, 1973).

Local contrast effects have not only been found in behavioural contrast studies. The frustration effect in the Amsel double alley and the Pavlovian positive induction effects are similar if not identical phenomena. In the Amsel double alley rats run faster in the second alley following nonreinforcement than following reinforcement in the first alley (Wagner, 1959; Robinson and Clayton, 1963; MacKinnon and Amsel, 1964; Amsel and Ward, 1965; Leonard et al., 1968; Ison and Krane, 1969; Staddon and Innis, 1969; Staddon, 1970; Hug, 1970; Fox et al., 1970; Kello, 1972; Benefield, 1974; Cross and Boyer, 1974); whether the effect is transient or permanent depends on the presence or absence of discrimination learning: when the subject can not know when reinforcement is omitted, the effect persists indefinitely (Amsel and Roussel, 1952; Amsel and Ward, 1965).

Positive induction is the term used by Pavlov (1927/1960) to describe an exaggerated conditioned response elicited by a CS+ when this CS+ was immediately preceded by a CS-. This effect, again, disappeared with prolonged discrimination training, i.e. as soon as the discrimination was mastered (e.g. Senf and Miller, 1967).

With respect to the local contrast effects found in multiple schedules, it is suggested that the overall behavioural contrast effect (to be considered below) depends on the conditioning of the local contrast effect to the unchanged component's stimulus situation (Mackintosh, 1974b). Others agree with the weaker claim that local contrast may contribute to the overall behavioural contrast effect under some circumstances, as there is often found a strong relationship between local and overall effects (Green and Rachlin, 1975; Spealman, 1976; McLean and White, 1981). This is not to say, however, that there is a necessary relationship, as this relationship is not always found and overall behavioural contrast does occur without any sign of the local effect (Boneau and Axelrod, 1962; Nevin and Shettleworth, 1966; Ellis, 1970; Mackintosh et al., 1972; Malone, 1976; Williams, 1976b; Schwartz, 1978; Hamilton and Silberberg, 1978; Rowe and Malone, 1981; Williams, 1979, 1981).

As Williams (1983) rightly remarks, the overall behavioural contrast effect is one of the most heavily investigated topics in the free operant research in the past 20 years. This research has been strongly biased towards pigeons as subjects and the positive contrast effect. As already stated, the behavioural positive contrast effect has been claimed to be restricted to pigeons (Freeman, 1971; Hearst and Jenkins, 1974). This claim is fully unjustified as behavioural positive contrast effects have been demonstrated in rats in many studies (Padilla, 1971; Beninger, 1972; Henke, 1972; Henke et al., 1972; Dickinson, 1972; Mackintosh et al., 1972; Wilkie,

1972; Jensen and Fallon, 1973; Uhl and Homer, 1974; Beninger and Kendall, 1976; Gutman et al., 1975; Allison, 1976; Henke, 1976; Gutman, 1977b; Bradshaw et al., 1978; Henke, 1979; Howard, 1979; Nallan and McCoy, 1979; Blough, 1980). Behavioural contrasts have also been found in goldfish (Ames and Yarczower, 1965; Bottjer et al., 1977), turtles (Pert and Gonzalez, 1974), crows (Powell et al., 1978) and even humans (Rovee-Collier and Capatides, 1979; Waite and Osborn, 1972), but not in squirrel monkeys (Spealman, 1978).

Traditionally, in a behavioural contrast experiment reinforcement in the variable component is shifted to zero (i.e. extinction) and therefore the emphasis has been on positive behavioural contrast effects, even to the extent that these were considered the behavioural contrast effects (Dunham, 1968; Freeman, 1971; Mackintosh, 1974b; Schwartz and Gamzu, 1977). The question of a possible negative behavioural contrast effect apparently did not arise. Consequently, the negative contrast effect has been investigated rather sparsely, though in the first behavioural contrast studies both positive and negative contrast effects were demonstrated (Reynolds, 1961a, 1961b, 1963). Undoubtedly, the negative contrast effect is a very real effect (Rachlin, 1973; Schwartz, 1975; McSweeney, 1978; Hellenthal and Marcucella, 1978; Rashotte, 1979b; McSweeney et al., 1981).

Contrary to the local contrast effects, the overall behavioural effect is an effect which persists as long as exposure to the differing schedules is continued. In this respect, as in others, it closely resembles the simultaneous contrast effect (Maxwell et al., 1969; Rilling et al., 1969; Hearst, 1971).

Behavioural contrast studies generally vary schedule of reinforcement (i.e. frequency, probability) and, as said, positive contrast effects are readily found. If quantity of reinforcement is varied, i.e. size of each individual reinforcer or duration of access, contrast effects may or may not occur (Shettleworth and Nevin, 1965; Brownlee and Bitterman, 1968; Kramer and Rilling, 1969; Baltzer and Weiskrantz, 1970; Padilla, 1970, 1971; Mackintosh et al., 1972; Gonzalez and Champlin, 1974; Madigan, 1978; Baltzer et al., 1979). Quality and delay of reinforcement are parameters not much studied in this context (Keller, 1970; Richards and Marcattilio, 1978; Norman, 1980; Fagen and Rycek, 1980).

Behavioural contrast effects have been found with different responses (keypeck, treadlepress, barpress, lickrate). It has been suggested for a long time that behavioural contrast was less reliably demonstrated in rats because of different response requirements: barpress instead of pigeon's keypeck (Hemmes, 1973; Westbrook, 1973; see also section 2.5.2 of this Chapter). This claim fails to hold up as shown by the many previously cited studies demonstrating behavioural contrast effects in rats. It may well be so that different responses are differently sensitive to the contrast manipulations (Jenkins, 1977; McSweeney, 1978; Davison and Ferguson, 1978; McSweeney, 1983); nevertheless, behavioural contrast effects have been found with various responses despite those differences.

One additional variable remains to be mentioned because it has provoked heated discussions. Stimulus location has been considered a crucial determinant of behavioural contrast: the effects would not occur unless the stimulus was localized on the response key (e.g. Keller, 1974; Redford and Perkins, 1974; Schwartz, 1974, 1975; Franczak, 1976; McSweeney, 1977; Bottjer et al., 1977; Woodruff, 1979). This claim has fallen through also, not only in studies showing behavioural contrast effects in rats, but also in studies with pigeons using diffuse stimuli or

special stimulus keys or no discriminative stimuli at all (Catania, 1973; Hemmes, 1973; Bouzas, 1976; Bouzas and Baum, 1976; Hearst and Gormley, 1976; White and Thomas, 1979; Williams and Heyneman, 1981).
In conclusion then, there are two types of contrast to be distinguished in behavioural contrast studies. First, there is the often but not always found local contrast effect, which is transient in nature and depends on the stage of discrimination learning the subject is in. Both a positive and negative contrast effect may be found. Secondly, there is the behavioural contrast proper. Data are skewed towards a positive contrast effect, but this is mainly due to experimental tradition. Most studies devised to detect negative contrast effects were able to do so.

2.4. Relationships between the various types of contrast

In the foregoing short survey many aspects of contrast effects have not been considered, e.g. transsituational contrast, choice contrast, contrast with aversive reinforcers or intracranial stimulation, and the contrast-related phenomena of peak-shift and schedule-induced polydipsia. The many reviews referred to often also deal with some of these topics.
The term contrast effect describes a number of different phenomena which may or may not represent the same psychological event. Results are often as variable as the procedures involved and generalizations are severely hampered by these procedural differences. Moreover, research has become so massive that it is difficult to see the wood for the trees. If contrast phenomena are not a unitary phenomenon, they may be attributed to several different effects, all of which may be operative in any particular situation. Our present state of knowledge does not yet permit us to unambiguously decide whether they should be subdivided, and if so along which lines.
In the next sections similarities and dissimilarities between the various types of contrast distinguished so far will be examined.

2.4.1. Successive versus simultaneous contrast effects

Within the class of incentive contrast effects, the drawing of a dividing-line is relatively easy. Even though the successive and simultaneous contrast effects may parallel one another in showing abundant evidence for a negative contrast effect and a somewhat less easily found positive contrast effect, there is general consensus that both contrast effects do not only result from very different experimental manipulations, but also represent different phenomena. In this light, it may well be considered remarkable that, almost without exception, both phenomena are brought together and are discussed in one and the same review article, leaving out the behavioural contrast procedure which has many similarities with the simultaneous variety (see below; Black, 1968; Bitterman and Schoel, 1970; Cox, 1975; Flaherty, 1982).
Arguments for separating the successive and simultaneous effects as different phenomena may be partly deduced from the foregoing (2.3). The paradigms used differ greatly: the successive procedure changes reinforcement conditions only once; the simultaneous design involves differential conditioning to repeatedly shifted stimulus conditions associated with different reinforcement values within a single session.
Then, simultaneous contrast effects develop slowly and are relatively

permanent, the successive contrast effect typically appears abruptly and wanes over a number of days. The simultaneous effect may be found under a much wider range of responses and reward variations than the successive variety.
Most straightforward are the results from a comparative point of view. The successive contrast effect has only been shown in rats, whereas the simultaneous contrast effect has been demonstrated in rats, pigeons, turtles, fish and monkeys. In this respect, the successive contrast effect shows some relationship with the partial reinforcement extinction effect (PREE). If subjects receive partial reinforcement (say 50%) during training, their resistance to extinction seems to increase (e.g. Bolles, 1975b). This effect, however, has only been found in rats and not in fish and turtles (Gonzalez et al., 1967; Pert and Bitterman, 1970; Mackintosh, 1971; Gonzalez et al., 1972). Thus, species which do not show the PREE also do not show the successive contrast effect. Perhaps the extinction paradigm might be considered a special case of a successive contrast paradigm. (For a review, see Bitterman and Schoel, 1970; Robbins, 1971; Bitterman, 1975, 1976).
Taking all evidence together, it seems safe to conclude that both types of incentive contrast effects, successive and simultaneous respectively, do not arise from the same processes.

2.4.2. Local versus overall behavioural contrast effects

As things are, matters are also clear in the case of behavioural contrast effects. Even though the local and the overall behavioural contrast effects may not always be entirely independent (see 2.3.3), they can be differentiated (Dunham, 1968; Mackintosh, 1974b; Rashotte, 1979b; McSweeney et al., 1981; Williams, 1983). That this is not always done, neither in experimental reports nor in reviews, may partly account for the often conflicting data reported.
For one thing, the behavioural contrast proper is maintained long after the local effect has disappeared. Secondly, the local contrast effect heavily depends on the discriminability of stimuli used and/or the stage of discrimination learning the subject is in: it is only apparent if discrimination between stimuli is difficult and/or while the subject is mastering the discrimination task; it disappears with sufficient training (see 2.3.3). Thirdly, the local contrast does only occur in close proximity with the foregoing stimulus: the interval between stimulus presentations may not exceed two minutes (Mackintosh et al., 1972). This is also illustrated by the fact that a local contrast effect in the unchanged component is only found if this unchanged component follows the presentation of a variable component, but not if it follows another presentation of the unchanged component (Boneau annd Axelrod, 1962; Terrace, 1966a; Vieth and Rilling, 1972; Rachlin, 1973; Benefield, 1974; Mackintosh, 1974a; Malone, 1976). On the other hand, the overall behavioural contrast -most interestingly- may also be induced by the component that follows. Thus, contrary to the local contrast effect, the overall behavioural contrast effect may result from an anticipated change in reinforcement conditions (Wilton and Gay, 1969; Williams, 1976a, 1979, 1981; Flaherty and Checke, 1982). If in a 3-component multiple schedule reinforcement rate during the middle component was varied, while the schedules during the first and third components were constant and equal, much stronger contrast effects were produced during the first than during

the third component (Williams, 1981). Thus, after repeated presentations of this multiple schedule, an anticipatory effect was found in the first component of the schedule.

2.4.3. Simultaneous versus behavioural contrast effects

Notwithstanding the many similarities, the use of mainly multiple schedules in the behavioural contrast paradigm has tended to keep it isolated from the simultaneous contrast effect studies. The results obtained with the behavioural contrast paradigm are generally reviewed separately without any reference to a possible relationship with simultaneous effects (Freeman, 1971; McSweeney et al., 1981; Williams, 1983), and vice versa (Black, 1968; Bitterman and Schoel, 1970; Bolles, 1975a; Cox, 1975).
As Gonzalez already concluded, the simultaneous contrast effect seems to be different from the successive variety; however, it seems to vary together with behavioural contrast effects (Bernheim and Williams, 1967; Gonzalez and Champlin, 1974; Pert and Gonzalez, 1974).
There are of course some obvious differences: simultaneous contrast paradigms employ rats as subjects, use discrete trial situations, measure latency or speed more often than not, and vary magnitude of reinforcement. Behavioural paradigms usually have pigeons for subjects, use free operant multiple schedule paradigms, in which the intertrial interval is zero, measure response rates and vary schedule of reinforcement. Moreover, subjects have to be extensively trained in the behavioural contrast paradigm and usually receive nondifferential training prior to the shift-phase, which gives this paradigm some characteristics of the successive contrast procedure. Finally, the behavioural design employs within-Ss comparisons and the simultaneous procedure uses between-Ss designs.
So far the differences. There are also many similarities. Both involve differential conditioning: different conditions of reinforcement are correlated with different stimuli. If experiments are designed that cut across the above-mentioned procedural distinctions, many of the differences in results obtained by both procedures, disappear (e.g. Brownlee and Bitterman, 1968; Padilla, 1971; Gonzalez and Champlin, 1974; Weinstein, 1977a). Other similarities may be seen in the influence of the intertrial interval: both types of contrast decrease with an increase in ITI; in the gradual development and subsequent persistance of the effects; and finally, in the phyletic generality of both types of contrast effects (see 2.3). Therefore, the least that can be said, is that the behavioural and the simultaneous contrast effects, may be more than superficially related.

2.5. Current state of affairs in the contrast research: theoretical developments

To complete this general survey of contrast phenomena, the main theories generated to account for the various reward-shift effects will be considered (see also Table 2.2). This is done to give an impression of which directions the explanations are sought in. An evaluation of the merits of each theory is beyond the scope of the present review.
As might be deduced from the foregoing, it is a point of discussion whether a theory should encompass all classes of contrast effects and should pretend to explain the whole mass of often contradictory results. In

section 2.3 and 2.4 it has been shown that different procedures and different measures do not always yield similar results from apparently similar operations. Besides, several different effects may have been given the common label of contrast. In that case, it is no easy reduction of all factors influencing the phenomena under consideration to a few well defined principles. Indeed, many consider it entirely impossible, as it is increasingly clear that not all contrast effects represent the same psychological event. Thus, "any attempt to attribute them to the operation of a single principle seems a singularly inappropriate goal" (Mackintosh, 1974b).
Until recently, successive and simultaneous contrast effects have often been considered closely related phenomena, because of similarities in both procedures used (rats, discrete trials, latency measures) and results obtained (an easily found negative and a somewhat more elusive positive contrast effect). Thus many theories proposed in the past have tried to encompass both classes of contrast effects. Conversely, the obvious procedural differences in the behavioural contrast studies (pigeons, multiple schedules, rate measures) and their results (mainly positive contrast effect), added to their being firmly embedded in the general context of free operant research, have kept their theoretical speculations isolated from those concerning the above-mentioned incentive contrast effects. It must be remembered, however, that evidence is accumulating that this supposed similarity between successive and simultaneous effects does not exist, whereas the differences between behavioural and simultaneous effects are not as large as has been suggested.

Theoretical developments may easiest be traced by consulting the various reviews of the literature that have appeared over the years (Black, 1968; Dunham, 1968; Premack, 1969; Bitterman and Schoel, 1970; Freeman, 1971; Mackintosh, 1974b; Cox, 1975; Bitterman, 1975; Black, 1976; McHose and Moore, 1976; Schwartz and Gamzu, 1977; Rashotte, 1979b; McSweeney et al., 1981; Flaherty, 1982; Williams, 1983). Initially, this literature provided little evidence for symmetrical effects. It is understandable, then, that this pattern of data had implications for the interpretations of reward shift effects, in that theories implying symmetry were not favoured. In the light of the evidence that for almost any contrast paradigm the one effect is still found much more readily than its opposite, many researchers still think it inappropriate to construct symmetrical accounts.

2.5.1. Incentive contrast effects

The successive contrast effect is the oldest known contrast effect and its most well-known study is the one by Crespi (1942), which forced Hull to change his ideas that different reward values create different habit strengths, into the idea that different reward values influence incentive motivation differently; thus, the influence was no longer thought to be on learning, but on performance. Incentive motivation itself was thought to be based on S-R learning: fractional anticipatory goal responses forming the basis of Pavlovian contingencies in the context of instrumental learning tasks. This S-R theory is an "absolute" one in that it assumes that the behavioural effects of a given reward depend entirely on its physical characteristics. More importantly, it is unable to explain any contrast effect, unless -as Spence did (see Bolles, 1975b; Flaherty, 1982)- it is assumed that reductions of reward value result in

frustration-induced responses which interfere with the instrumental response and hence create negative contrast effects. As the positive contrast effect was considered an artefact, no opposite mechanism was needed.

Early work demonstrating negative contrast effects encouraged theories which combined Tolman's concept of **expectancy** with S-R theory in one way or another. For example, Black (1968) assumed that behaviour in the runway is determined by the "effective excitatory potential" ($\overline{E}$), where $\overline{E}$=E-I; E, excitatory potential, or the tendency to run, increases whenever this response is reinforced; I, inhibition of the running responses, is incremented whenever a reinforcement smaller than what was expected, occurred. Just as S-R theory did, Black also assumes that E is an absolute function of reward value. Like S-R theory, Black's **inhibitory conditioning** model was developed in the conviction that a positive contrast effect did not exist. Unlike S-R theory, his constructs seem to explain both successive and simultaneous negative contrast effects.

Largely developed to explain successive negative contrast effects, the **generalization decrement** theory reasons that whenever an animal is tested under conditions that depart in some way from those under which it was trained, decrements in performance will occur. When reward values are changed, the stimulus situation has changed; new stimuli are produced and hence performance is disrupted due to generalization decrement (Spear and Spitzner, 1966; E.J.Capaldi and Lynch, 1967; E.J.Capaldi, 1967, 1972; E.J.Capaldi and Ziff, 1969). Even though this theory has much empirical support, it cannot satisfactorily explain the effects of deprivation, repeated shifts, novel stimuli etcetera.

A concept related to generalization decrement is the concept of **neophobia** (Lombardi and Flaherty, 1978; Lombardi, 1979, 1980; Flaherty et al., 1980; Meinrath, 1980). Generalization decrement seems to refer entirely to learned responses, neophobia on the other hand does not imply this and carries emotional connotations. Neophobia, as all models considered before, can only account for the negative contrast effect, and particularly the successive negative contrast effect. There is some evidence that neophobia may be the principal cause of contrast on the first post shift day, whereas other processes should be involved on subsequent days (Lombardi and Flaherty, 1978; Meinrath, 1980: Flaherty, 1982).

Attempts to interpret the negative contrast effect in terms of emotional concepts, have a long tradition. Elliot (1928) and Tinklepaugh (1928) both used emotional terms to describe the behaviour of their animals after a change from a preferred to a nonpreferred reward. Crespi's (1942) terms "elation" and "depression" also carry clear emotional connotations; Spence needed the concept of disruptive emotional responses (see before) to explain negative contrast effects. And finally, Bower (1961) linked the negative contrast effect to Amsel's (1962) **frustration** theory. Here the idea is that lowered performance after shift is the result of a conflict between anticipation of reward and anticipation of frustration; frustration occurs because of generalization of anticipation of the large reward from S+ to S- (Bower, 1961; Spear and Spitzner, 1966; Ludvigson and Gay, 1967; Daly, 1974a, 1974b; Calef et al., 1978; Flaherty et al., 1978; Flaherty et al., 1979b; Calef et al., 1980).

Table 2.2. Summary of the main theoretical constructs used to explain contrast effects. For each model a few representative papers are given, plus the effects considered "explained". NCE: negative contrast effect; PCE: positive contrast effect.

THEORETICAL CONSTRUCTS	AUTHORS	SUCC. CONTRAST	SIMUL. CONTRAST	BEHAV. CONTRAST
S-R Associations	Hull, 1943, 1952; Spence, 1956	NCE		
Inhibitory Conditioning	Black, 1968	NCE	NCE	
Generalization Decrement	E.J.Capaldi, 1967 Spear and Spitzner, 1966	NCE		
Neophobia	Lombardi, 1979, 1980	NCE		
Frustration	Amsel, 1962, 1967, 1980 Bower, 1961; Bloomfield, 1969, 1972; Gonzalez and Champlin, 1974	NCE	NCE	PCE
Adaptation Level	Bevan and Adams, 1960 Bevan, 1963; Helson, 1964	NCE PCE	NCE PCE	
Incentive Averaging	McHose, 1970 McHose and Peters, 1975 McHose and Moore, 1976	NCE PCE		
Reinforcement Level	E.J.Capaldi, 1974, 1978	NCE PCE		
Response Suppression	Terrace, 1966a			PCE
Relative Frequency of Reinforcement	Reynolds, 1961a			NCE PCE
Behavioural Competition	Hinson and Staddon, 1978 Staddon and Simmelhag, 1971; Staddon, 1982			NCE PCE
Additivity or Autoshaping	Rachlin, 1973 Gamzu and Schwartz, 1973 Hearst and Jenkins, 1974			(NCE) PCE
Rebound	Williams, 1965 Mackintosh, 1974b			local NCE local PCE

This frustration produces disruptive emotional responses; hence, this theory is sometimes termed the **competing response** theory. The frustration interpretation can incorporate many of the negative contrast findings, successive as well as simultaneous. It has also been argued that it is frustration that produces the behavioural positive contrast effect; if the variable component of a multiple schedule is extinguished, this will result in frustration. Enhanced responding in the unchanged component might reflect a release from a frustrating situation (Bloomfield, 1969; Scull et al., 1970; Bloomfield, 1972; Scull, 1973; Mackintosh, 1974b). As Gonzalez and Champlin (1974) suggested, the positive behavioural contrast effect might be based upon an unconditioned form of frustration, whereas the simultaneous and successive negative contrast effect might result from a conditioned or learned form of frustration.

All theories considered so far have been essentially **absolute** and **asymmetrical**. An alternative view was presented by "relative" models which maintain that the behavioural effectiveness of a reward is not determined solely by its physical aspects but -at least partially- depends upon its "perceived value", i.e. is influenced by the context of that reward. Major implications of this kind of theories are, first, that contrast effects are symmetrical, and secondly, that the effects are not permanent, as repeated exposure to the changed reward value should also alter the perceived value of these reward events. This symmetry has long been considered a weakness in the theory in the past (Black, 1968; Dunham, 1968; Mackintosh, 1974b), but now is considered an asset (Flaherty, 1982), as data concerning the viability of successive and simultaneous positive contrast effects are accumulating.

The oldest and probably best-known of these relative models is the **adaptation-level** theory (Bevan and Adamson, 1960; Bevan, 1963; Helson, 1964; DiLollo, 1964b; Bevan, 1966, 1968; Malone, 1975). Its central assumption states that subjects continuously pool all relevant information about a particular stimulus to form a norm or adaptation level, which is used as a standard for later judgments. For example, subjects judge current reward values by comparing them with an adaptation level formed on the basis of past or concurrent experiences with other reward values (Flaherty, 1982). This judgment might arise from purely sensory interactions. Some contrast effects obtained with sucrose solutions might be mediated principally by peripheral sensory processes (Flaherty and Largen,1975; Flaherty and Sepanak, 1978; Flaherty and Kaplan, 1979; Flaherty, 1982). But it certainly cannot explain everything.

A more recent relative model is E.J.Capaldi's (1974, 1978) **reinforcement-level** theory. This theory assumes also that it is the discrepancy between expected and obtained reward that results in the occurrence of contrast effects. The model goes further in that it postulates some specific, purely associative, processes by which contrast is produced. Thus, the reinforcement level determines the strength of S-R associations or habits. If obtained reward is greater than expected, a contrast effect results because of a greater accumulation of habit strength for the up-shifted subjects; for down-shifted animals the discrepancy between expected and obtained reward results in an accrual of inhibition, that, in turn, leads to depressed responding (Capaldi, 1974). Thus, discrepancies between expected rewards and obtained rewards possess specific properties, such that associative tendencies are strengthened when obtained reward exceeds expected reward, and response inhibition accrues when expected reward exceeds obtained reward.

Superficially related to the foregoing is the **incentive averaging** model of McHose (1970; McHose et al., 1972; Hulse, 1973; McHose and Howard, 1973; McHose and Peters, 1973, 1975; McHose and Moore, 1976) which concentrates on successive contrast effects only. Contrary to E.J. Capaldi, in his model McHose does not make use of contextual influences that modulate the perceived value of rewards. Thus, his concepts do not carry the connotation of a perceptual judgment. McHose assumes that the average incentive value of a given reward schedule is a function of the incentive values established by the different reward values contained in that reinforcement schedule. Consequently, subjects "average" their reward expectancies across the absolute values of the rewards obtained. A recent addition to his theory is the concept of **salience**. The salience of a stimulus depends on the number of times that stimulus has preceded the reinforcer and on the intensity of the stimulus in relation to that of other stimuli. As the salience of expectancy-based cues (K) increases, the relative amount of associative tendencies or habit strength (H) accrued to K increases also, at the expense of the salience of and habit strength accrued to other situational cues (A). The salience of expectancy-based stimuli (K) is assumed to be specific to the characteristics of the reinforcer used. Subjects receiving large rewards will accrue more habit strength to expectancy-based stimuli (K) relative to other situational stimuli (A), than subjects receiving small rewards. When the small reward group then is shifted to a large reward, the habit strength accrued to large reward expectancy cues (K) will eventually become equal to that of the large reward group. However, initially, the relative amount of habit strength which in the preshift phase has accrued to the other situational stimuli (A), for the shifted group exceeds that of the large reward group. Thus, the result is a positive contrast effect. Positive as well as negative contrast effects arise as a result of the fact that the shifted groups accrue different levels of habit strength to other situational cues in the preshift period, than the control groups. The degree of the contrast is proportional to the difference between the postshift reinforcer and the average incentive value of the preshift reinforcer.

2.5.2. Behavioural contrast effects

All the above-mentioned theories have adressed themselves to incentive contrast effects exclusively, the only exception being the concept of **frustration** which in its unconditioned form has been considered the cause of the enhanced responding of the behavioural positive contrast effect (Gonzalez and Champlin, 1974). Theories accounting for behavioural contrast effects have, however, mainly developed without much points of contact with the incentive contrast literature.
In the early days of behavioural contrast research it was suggested that the positive contrast effect was a "by-product" of those discrimination procedures that allow one stimulus (S-) to acquire inhibitory/aversive properties (Terrace, 1966a, 1971; Brownstein and Hughes, 1970; Rashotte, 1979b). This inhibitory stimulus after its termination leaves a kind of after-effect that invigorates responding during the following S+. Thus far, the idea resembles the above-mentioned frustration effect. It goes further than that, however, in maintaining that S- acquires inhibitory or aversive properties only if actual responses have to be withheld/inhibited. **Response suppression**, i.e. a change in the rate of responding, has been considered an important determinant of behavioural positive contrast.

However, it has repeatedly been shown that it is neither a necessary nor a sufficient condition for the occurrence of behavioural positive contrast effects (Bloomfield, 1967a, 1967b, 1972; Hemmes and Eckerman, 1972; Halliday and Boakes, 1972, 1974; Rilling et al., 1975; Kodera and Rilling, 1976; Boakes et al., 1976).

Reynolds (1961a) proposed that a change in the rate of reinforcement might be a sufficient condition for the behavioural contrast effects to occur. Since he had demonstrated both positive and negative contrast effects, his **relative frequenoy of reinforcement** theory accounted for both effects (Reynolds, 1961a, 1961b, 1961c, 1963). But whereas a changed rate of reinforcement reliably produces contrast effects, it does not seem to be a sufficient condition under all circumstances; and since there are circumstances for which other conditions suffice, it is not a necessary condition either for contrast to occur (Brethower and Reynolds, 1962; Terrace, 1968; Weisman, 1969).

Premack (1969) suggested a somewhat less precisely defined variable. Contrast should result if and only if there is a "change for the worse", or, a change in aversiveness associated with one of the components of the schedule. "Worse" is defined as any condition which -in a choice situation- is less preferred than the schedule in effect in the unchanged component (Premack, 1969; Bloomfield, 1969, 1972). The mechanism by which this change for the worse is translated into a positive contrast effect is not specified.

A very different approach introduces the concept of **behavioural competition** (Staddon and Simmelhag, 1971; Hinson and Staddon, 1978; Staddon, 1982). Its basic notion is that contrast in multiple schedules derives from the competition between interim (or nonrelevant) behaviours and terminal (instrumental) behaviours. When a multiple VI VI schedule is changed to a multiple VI EXT schedule, both types of behaviour disappear from the EXT-component. The interim behaviours occurring during the unchanged component can then move into the EXT-component, leaving more time for terminal (operant) responding in the unchanged component, so that an increase in response rate i.e. a positive contrast effect occurs. In other words, contrast might be considered to result from a change in time allocation (cf. White, 1978). A crucial assumption here is that the sum of interim and terminal behaviours is a constant. This behavioural competition theory is closely related to the Rachlin (1973) version of the additivity theory, to be considered below.

Quite a large body of contrast research has been devoted to testing **additivity**-theory, or **autoshaping**-theory. This theory has been presented in different forms by Gamzu and Schwartz (1973; Schwartz and Gamzu, 1977) and Rachlin (1973). All basically state that in multiple schedule situations two types of responses develop:

1. the instrumental response which is controlled by the response-reinforcer contingency, and
2. additional responses that are controlled by the stimulus-reinforcer relation (Gamzu and Williams, 1971, 1975; Schwartz et al., 1975).

Positive behavioural contrast occurs only when those two processes interact in such a way that responses controlled by the stimulus-reinforcer relation facilitate or add to the responses controlled by the response-reinforcer relation. In baseline training responding is controlled primarily by the operant response-reinforcer relations, because the two stimuli are associated with identical reinforcement schedules. When one stimulus (S-) now signals extinction, the other stimulus (S+) becomes a signal for the more favourable component of the schedule. It is the thus arranged

stimulus-reinforcer relation that by evoking additional responses, produces a positive contrast effect. It is apparent that -this theory being valid- contrast will depend heavily upon the use of a response which is strongly affected by classical conditioning contingencies (e.g. keypeck), as the evoked response must be of the same topography as the instrumental response for additivity to result. This at once reveals a few of the many weaknesses of additivity theory: a treadle press response with pigeons, or a lever-press response in rats (at least in those rats that press the lever with their paws rather than with their mouths) should reveal no positive contrast effect; also, using diffuse nonlocalized signals or separate signal keys should produce no positive contrast effect (see 2.3.3). However, in all cases a positive contrast effect can be obtained (e.g. Bradshaw et al., 1978a).

It should be noted that Rachlin (1973) and Hearst and Jenkins (1974) state that not only positive contrast effects but also negative contrast effects may be explained by classically conditioned responses that interfere with or subtract from the instrumental responses (compare also response-competition theory). However, at best, additivity theory appears to account only for the local variety of behavioural contrast, because most responses (keypeck) controlled by the stimulus-reinforcer contingency occur shortly after the transition from one component to the other; and even in the explanation of local contrast effects this hypothesis has its limitations (Rashotte, 1979b; Williams, 1983).

The theories on behavioural contrast considered before have either concentrated on the overall behavioural contrast effect or not differentiated between the overall and local variety. As has been noted, at least one, additivity theory, seems more applicable to the local contrast effect. The local contrast effect has also been interpreted as a rebound from inhibition and facilitation respectively, clearly reminiscent to Pavlov's (1927/1960) induction. Terrace (1966) has not been alone in suggesting that contrast effects are dependent on rebound effects of preceding stimulus presentations (D.R. Williams, 1965; Mackintosh, 1974). And -as noted in 2.3.3- the overall effect is sometimes seen as at least partially the result of a conditioning of the local effect (Mackintosh, 1974b), whereas others consider local contrast effects and overall behavioural contrast effects functionally independent (e.g. Malone, 1976; Williams, 1976b; Schwartz, 1978; Williams, 1983).

2.5.3. *Conclusions*

Research concerning contrast effects has become so massive that, as Williams (1983) puts it, reseachers seem to despair over sorting out the controlling variables. This is clearly reflected in the abundance and great variety of the constructs generated. This survey of theoretical developments is certainly not exhaustive. Only theories generating much research have been presented (see Table 2.2).

Thus far, no single theoretical account can deal adequately with all experimental data. However, it is questionable whether it should. As it is clear that contrasts may occur for several different reasons, several theories might be able to explain different sets of data. Also, they probably are not all mutually exclusive in that in many situations various factors might interact to determine the behavioural effects under study. It has been shown that various types of contrast effects exist; particularly the successive variety seems entirely different from the

others. Nevertheless, most theories proposed for the successive contrast effects pretend to explain the simultaneous contrast effects as well. On the other hand, despite the resemblance on many points of behavioural and simultaneous contrast effects, no model tries to deal with both. This may be so because behavioural contrast research is almost entirely preoccupied with the positive contrast effect, whereas simultaneous contrast studies concentrate on the negative contrast effect.

The many theoretical constructs fall into three groups, each emphasizing different factors. Only the adaptation-level theory in its original form is a purely sensory-perceptual model. Associative theories have been best represented; they have also been developed furthest towards more or less formalized models, which makes them readily testable. Emotional-motivational theories, on the other hand, have not been formalized at all and can hardly be verified or falsified.

Emotional factors certainly are involved in many of the effects considered. Besides, the concept of expectancy or incentive averaging is incorporated in many models in various ways, and appears to be a valuable construct.

This review has repeatedly stressed the importance of the topic of symmetry. Again, in the light of the historical accumulation of the evidence and the persisting reluctance to accept symmetrical contrast effects, the general one-sidedness of theoretical interpretations comes to no surprise. However, because evidence is also accumulating that both a negative contrast effect and a positive contrast effect can be obtained, this lack of symmetry may be considered a weakness.

In the next chapter the development of a contrast procedure that will enable us to investigate the existence of symmetrical contrast effects in one and the same test situation will be elaborated.

Chapter III

CHOICE OF EXPERIMENTAL PARADIGM

In Chapter I a few theories have been enunciated that postulate two opponent processes or systems to account for the regulation of the overt appetitive and aversive behaviours as shown by the organism with respect to affective stimuli. A second postulate proposes that the two opponent processes actualize this regulation in mutual interaction, either inhibitory (Dickinson and Dearing, 1979; Dickinson and Pearce, 1977) or excitatory (Solomon and Corbit, 1974) in character. According to Dickinson c.s. the opponent processes are activated by different classes of stimuli, whereas in Solomon and Corbit's model one single affective stimulus activates both (see Figure 1.2 and 1.3).

One method of investigating these postulated interactions, is to concentrate on events occurring at transitions of affective stimuli that have triggered the regulatory processes; in other words, to concentrate on stimulus terminations and their after-effects. The inhibitory interaction model does not explicitly deal with the effects of stimulus termination, but implicitly suggests the occurrence of rebound effects due to disinhibition. Presumably, the rebound effects will be proportional in size to the degree of inhibition induced by the affective stimulus.

In contrast, Solomon and Corbit proposed a homeostasis-related mechanism that develops slowly; from this pattern of growth it follows that the after-effects must be small at first but will increase over repeated presentations, whereas the effect of the affective stimulus itself will initially be large and will gradually diminish. Thus, effect and after-effect will never be proportional in size.

Whichever model is considered as best fitting the data, a central feature of both is symmetry. That is, a situation associated with aversive stimuli will be followed by a facilitation of appetitive behavioural after-effects, and vice versa. Our main objective, therefore, has been to search for evidence for this assumed symmetry. This, first of all, implied the use of appetitive and/or aversive stimuli that only differ in affective quality, so that interferences induced by other differences would not occur. It was decided to utilize taste stimuli, as palatability of food and water rewards can be easily changed in a direction that makes the rewards more attractive/desirable or more aversive/rejectable; moreover, interferences through changes in drive-level, as might occur when reward quantity is changed, are hopefully excluded: as the concentration of the sucrose solution we intend to use (8%) is rather low and only small volumes are offered per reinforcement, the caloric value of a single reinforcer probably does not substantially affect performance. It is well known that taste quality is a very conspicious aspect of rewards (Pfaffman, 1961, 1969, 1982); its influence on operant behaviour is also well-documented (e.g. Bolles, 1975a). Changes in palatability of reward result in increases or decreases in response level that can be unambiguously interpreted as reflecting approach or avoidance tendencies respectively that are exclusively controlled by the hedonic/affective changes in taste.

Secondly, our emphasis on symmetry implies certain procedural requirements. For the effects of appetitive as well as aversive stimulus changes to be detectable within a single situation and utilizing a single response measure, a certain behavioural base level has to be established that permits behavioural deviation in both directions. Thus, a free operant

responding situation was chosen as our basic test situation in the majority of our experiments and a runway situation was employed in the two remaining studies.

In Chapter II it was argued that the contrast paradigm is preeminently suited to explore the implication of symmetrical after-effects in the above-mentioned theories. The study of contrast is, in fact, concerned with exactly the type of transitions considered here. They do focus on confronting the subject with varying reinforcing events or stimuli associated with varying reinforcing events (shifts) in order to gain insight in the resulting after-effects (contrast effects, induction effects). Within the context of contrast research, too, the issue of symmetry is a sore subject. Initially, there was no consistent evidence for symmetry. The current state of affairs, however, is that generally both contrast effects, negative and positive contrast effects, can be obtained, but one always meets with more difficulties and requires more precautionary measures. Most theoretical interpretations of contrast effects do not account for symmetry. And the opponent process theories that offer models for affective behaviour, have never explicitly been applied in this context. It is true that the local contrast effect is interpreted as a rebound effect, but this only demonstrates that the rebound mechanism is an independent concept, not unique to the inhibitory opponent process model. Besides, the rebound interpretation has only some bearing on the local contrast effect, which is a very transient effect within as well as over sessions.

Apart form the issue of symmetry, particularly the contrast paradigms containing repeated shifts, i.e. the behavioural and simultaneous varieties, may offer the opportunity to shed some light on 1. the relation between effects and after-effects of changes in affective stimuli and 2. the potential changes in these after-effects over time. It has been demonstrated many times that the behavioural as well as the simultaneous contrast effects develop gradually, gain in strength and then persist for a very long time. This is, in fact, exactly what Solomon and Corbit's (1974) model predicts.

As has been stated in Chapter II, initially the results of behavioural and simultaneous contrast studies were definitely asymmetrical: the evidence for simultaneous positive contrast effect was scarce at best, and the reality of a behavioural negative contrast effect was hardly investigated. Considering the high degree of likelihood that this discrepancy in results can be attributed -at least partially- to methodological differences, we have decided to design a procedure that cuts across the behavioural-simultaneous distinction. Dissimilarities and similarities of the two main groups of contrast studies have been considered in Chapter 2.4. Here, it suffices to sum them up. Typical aspects of the two situations are:

	BEHAVIOURAL	SIMULTANEOUS
Subject	pigeons	* rats
Test	* free operant multiple schedule	* discrete trials runways
Intertrial interval	none	* ITI
Response measure	* leverpress rate	running speed/latency
Training	* baselevel pretraining	not needed
Shifts	schedule	* quantity
Comparisons	* within-Ss	* between-Ss

Both procedures have been combined in that
1. Rats were used in a free-operant multiple-schedule situation, requiring pretraining;
2. ITI's were introduced to create a discrete trial situation;
3. Quality and/or quantity instead of schedule was the shifted parameter;
4. Response rates were recorded and primarily compared between groups.

It is difficult to decide now whether this procedure should be termed a behavioural or a simultaneous contrast design as both have contributed several characteristics (marked with an asterisk).
As explicated before, all experiments have been designed essentially symmetrical.
In Chapter IV two experiments will be presented in which either quinine or sucrose was added to the liquid reward, thus changing the quality of the reward.
In Chapter V an experiment will be reported that partly replicates the foregoing and varies quantity of the liquid reward as well.
In Chapter VI two experiments will be reported which use a runway situation and measure latency/speed. Quality of reward (quinine or sucrose addition) and quantity of reward are varied. In the first experiment subjects are water-deprived and reinforcement consists of liquid rewards; in the second experiment subjects are food-deprived and obtain solid rewards.
In Chapter VII, finally, an experiment will be presented which was executed in collaboration with dr.C.Sennef. The procedure is mainly the one described in Chapter V, except that only quality of reward has been varied. Subjects have been lesioned in the medial and sulcal prefrontal cortex of the brain. The effects of this brain damage on behaviour with respect to shifts in the quality of reward and on the occurrence of contrast effects have been investigated. There are many indications that these parts of prefrontal cortex are involved in the regulation of appetitive and aversive behaviour (see also, Sennef,1985).

CHAPTER IV

CONTRAST EFFECTS AFTER SHIFTS IN THE QUALITY (PALATABILITY) OF A LIQUID REWARD

4.1. Introduction

Current motivational theories generally assume behaviour to result from the interaction of two opponent motivational systems or processes (Chapter I). The various incentive stimuli, in conjunction with activity in the appropriate motivational systems are thought to generate either appetitive or aversive behaviours (Bindra, 1976). The strength of the behaviours is postulated to be determined by the relative level of activity in two underlying neural structures or processes, one appetitive, the other aversive. These central appetitive and aversive processes are not considered independent (Solomon and Corbit, 1974; Dickinson and Pearce, 1977; Dickinson and Dearing, 1979). For the moment not taking into account the different views concerning the nature of the interactions between these two systems or processes, one conspicious feature of this type of theories is a requirement of symmetry: interactions between appetitive and aversive events are supposed to be symmetrical. Situations used in examining contrast effects seem preeminently suited to examine this hypothesized symmetry.

The evidence for symmetry in the contrast literature, however, is ambiguous (Chapter II). Whereas in pigeons the **behavioural** positive contrast effect is easily demonstrated (Mackintosh, 1974b; Rashotte, 1979b; McSweeney et al., 1981; Williams, 1983), much less is known about the behavioural negative contrast effect. The imbalance in the behavioural contrast data is, however, mainly caused by the fact that, due to procedural tradition, behavioural contrast studies have been almost exclusively concerned with the positive contrast effect. On the other hand, the **simultaneous** negative contast effect consistently occurs under a variety of conditions with rats; the simultaneous positive contrast effect can be found only when special arrangements have been made to produce it (Dunham, 1968; Black, 1968; Mackintosh, 1974b; Cox, 1975; Rashotte, 1979b; Flaherty, 1982).

As the behavioural and simultaneous contrast designs have many similarities, this contrasting pattern of results is surprising. It is not at all clear whether this discrepancy as well as the asymmetry of the results can be attributed to the procedural dissimilarities between the two groups of studies.

Therefore, our intent was to study contrast effects in a design that has features of both. Thus, in order to maximize the opportunities for symmetrical effects, rats were used in a free operant situation in a between-subjects design (see also chapter III). Rate of responding on a variable interval (VI) schedule was taken as a measure of preference for different types of reinforcers in water-deprived animals. It is well known that barpress rates reflect the effects of variations in reinforcement (Pfaffman, 1961; Mackintosh, 1974b; Bolles, 1975a; Rashotte, 1979a). And it has often been stated that especially VI schedules maintain a stable level of responding during long test sessions (Ferster and Skinner, 1957; Nevin, 1973).

Quality of reward, more specifically palatability, rather than amount, was chosen as the parameter of reinforcement to be shifted. Using taste as the parameter was assumed to offer the advantage of not running into problems

caused by contaminations with changes in drive intensity, time needed for consumption etcetera, as might occur with changes in quantity of the reward. Apart from this, studies concerning learned taste-aversion clearly demonstrate that taste is a rather conspicious aspect of reinforcement for rats (Bolles, 1975a; Pfaffman, 1982). The hedonic quality of taste may be among its most fundamental properties (Pfaffman, 1961). Also important, however, taste is a quality which can easily be changed in negative as well as positive directions.
Two experiments will be reported that both are designed to reveal symmetrical contrast effects. In the first experiment a quinine solution was contrasted with water as a reward and the occurrence of positive as well as negative contrast effects was investigated. In the second experiment, which was essentially a replication of the first, a sucrose solution was employed, and again attention was focused on the presence or absence of positive and negative contrast effects.

4.2. Experiment I. Water versus quinine

In the first experiment to be reported, the conventional tap water reward was alternated with a water reward which was made bitter by adulteration with quinine. A variable interval (VI) schedule of reinforcement was used to prevent different rates of responding to result in substantial differences in total amount of reward consumed. During sessions various intrusions of reinforcement changes, i.e. shifts, were given; the resulting procedure might be considered a behavioural contrast procedure, with shifts in quality of reward instead of shifts in schedule of reinforcement. A between-subjects (simultaneous) design was chosen. Thus the procedure might also be considered a simultaneous paradigm.

4.2.1. Material

Subjects
Subjects were 34 experimentally naive male albino Wu rats (SPF63 Cpb; Loosli, 1975), obtained from the Central Institute for the Breeding of Laboratory Animals (TNO), Zeist. They weighed about 295 g at the start of the experiment. They were housed individually in Macrolon cages (23x35x16 cm) and had free access to food throughout the study. They were kept in a stock room adjacent to the experimental room under reversed day/night schedule. All testing took place during the dark period. 10 Ss served as a reference group when fluid intake was measured in the home cages, the other 24 subjects were used in the contrast experiment.

Apparatus
Four standard operant-conditioning chambers (Campden, model 410) were used. Each chamber normally contains two levers, but the lever near the backside panel was removed. A force of 8 grams was required to activate the lever. The reward of .1 ml of liquid was presented by a dipper during 6 sec. Each skinnerbox was mounted in a sound attenuating cubicle; its frontwall was left open throughout the experiment to facilitate within-session changes in the reinforcer during the shift sessions. The exhaust fan served ventilation purposes and masked ambient noise (65 dB). On the ceiling of the testing cage a speaker was mounted through which tone signals could be delivered. Standard scheduling and recording equipment was located in the

same room. The room was illuminated by a dim red light.

4.2.2. Procedure

Quinine intake and baseline training
Following several days of adaptation to a water deprivation schedule (22 1/2 hr), 24 subjects were shaped and trained to press a lever for continuous water reinforcement during 15-min sessions. After the training session they had access to water in their home cages during one hour. Sessions were given on four successive days per week.
On four successive non-training days subjects were offered 10-min. presentations of a .01% quinine solution (QHCL, weight/volume in tap water) in their home cages, and amount of quinine consumed was recorded. This was done to exclude the possibility of flavour neophobia to influence responding later on in the experiment (Domjan et al., 1976; Best et al., 1978; Flaherty et al., 1980). The quinine concentration chosen is known to be aversive for rats, but not so aversive as to prevent them from consuming it when thirsty (Oakley, 1965; Stevens, 1969; Rowland and Flamm, 1977). Another group of 10 rats was given 10-min presentations of tap water as a reference: the latter did not participate in the remainder of the experiment.
After 8-10 sessions of CRF training, subjects were assigned to one of two groups; group W continued to leverpress for water, whereas group Q from now on received the .01% quinine solution as a reward. At this moment, one subject had to be discarded because he did not learn the leverpress response. After another CRF session and two FR-5 sessions, the schedule was changed to an arithmetic VI-30 sec schedule with intervals ranging from 10-50 sec in steps of 5 sec. That is, reinforcement was delivered for the first response made after a varying interval with a mean duration of 30 sec; delivery of reinforcement did reset the clock to zero. At the same time session length was increased to 30 minutes. This regime stayed in effect throughout the remainder of the study. VI-30 sec training continued until performance appeared to be relatively stable, requiring 22 sessions. Each group was subsequently subdivided; the subjects in each group were matched according to their response rates in the four last sessions of VI-30 sec training; one of each pair was randomly assigned to the experimental groups QW or WQ and the other to their respective control groups QQ and WW. Each group contained six subjects, with the exception of group WW which had only five. At this moment shift sessions started.

Shifts in taste of reward
A session was divided into seven periods of 4 minutes each, resulting in a total session duration of 28 minutes (see Figure 4.1). Each subject started with a 4-min period in which its usual reward, water or quinine, was given as before. During the second and also during the fifth period the experimental groups were exposed to a shift in the reinforcer: for group WQ the water reward was changed to the .01% QHCL solution, whereas for group QW the quinine reinforcer was exchanged for pure unadulterated water. This change in reward was cued by a train of click tones of 1.000 Hz, 8 dB above background noise, which lasted as long as the change was in effect.

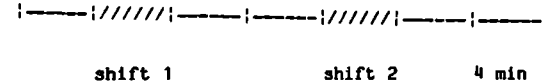


Figure 4.1. A shift session represented graphically.

At the end of each shift period subjects were shifted back to their usual rewards for the next two periods. For the control groups WW and QQ, which received the same reward as before throughout the session, the fluid-trays were pseudo-exchanged only at the beginning and end of the second and fifth periods, and the clicking tone signal was on during these periods. This procedure was repeated for 10 sessions, one session each day. Response rates were registered automatically every minute.

4.2.3. Results

Quinine intake in the home cage during 10-min presentations
As can be seen in Table 4.1, on all four days animals which had access to the QHCL solution drank less than a reference group which received water on all four days. After the second day water intake did not show further increases, whereas QHCL intake did. All days taken together, subjects given the quinine solution drank a mean volume of 3.0 ml per day only and the reference group consumed a mean 7.4 ml of water.

Table 4.1. Group mean fluid intake (ml) during four 10-min presentations in the home cage.

	QUININE n=24		WATER n=10	
DAYS	$\bar{X}$	SE	$\bar{X}$	SE
1	1.2	0.2	2.9	0.9
2	2.2	0.3	8.1	1.3
3	2.9	0.6	8.0	0.9
4	5.2	0.6	7.9	0.9

Table 4.2. Mean response rates and mean reinforcement rates per session, computed from the last 5 sessions of VI-30 sec training. Rates were averaged per group per day.

	QUININE n=12		WATER n=11	
	$\bar{X}$	SE	$\bar{X}$	SE
Response Rates	336	14	537	20
Reinforcement Rates	35	0.4	40	0.6

Baseline training

Following an initially strong increase in VI-30 sec responding, from the tenth session of VI training onwards response rates did not change substantially (Table 4.2). Response rates for the quinine group were depressed compared to those for the water group, as was to be expected from the fluid intake scores in the home cages.

The number of reinforcements each group received (Table 4.2) remained very stable over days. The water group got slightly more than the quinine group due to the higher response rates in this group.

On the data of the last 5 baseline sessions multivariate trend analyses (Finn,1977) were performed, comparing each experimental group with its control group per period of 4 minutes. As was to be expected, the groups QQ and QW on the one hand, and the groups WQ and WW on the other hand, did not differ from each other. In all periods trends over days were absent, except for period 4 (multiv. $F=4.37$; $df=4,16$; $p<.01$); the cubic trend component explains some 80% of this effect and can be attributed to a lowered response rate in period 4 during the sessions 3 and 4 in the groups WQ and WW. In none of the 7 periods did group WQ and WW significantly differ from each other with respect to trends; neither did the groups QW and QQ.

A VI schedule generally produces a relatively steady state of responding within a session. In our case, however, response rates steadily decreased during each session from a rather high rate at the beginning to a much lower rate at the end of each session. In contrast, the rate of reinforcement remained at a constant level throughout each session. Figure 4.2 depicts the mean response pattern during the last 5 VI-30 sec baseline sessions. The solid function represents the water group, the dashed line is the quinine group.

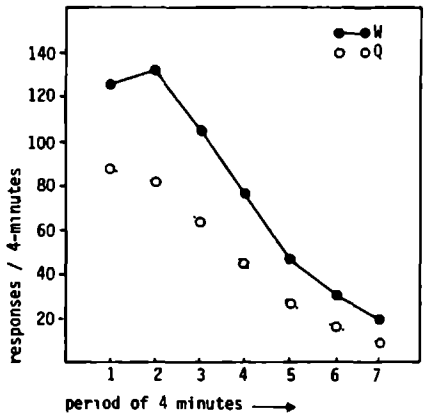


Figure 4.2. Mean response rates of the last 5 VI-30 sec baseline sessions, plotted per period of 4 minutes.

Shifts in taste of reward

Response rates are presented over individual subjects per period of 4 minutes.

The decline in responding within sessions, found already in baseline training, persisted throughout this phase of the experiment, although influenced by changes in performance caused by the shifts in reinforcers.

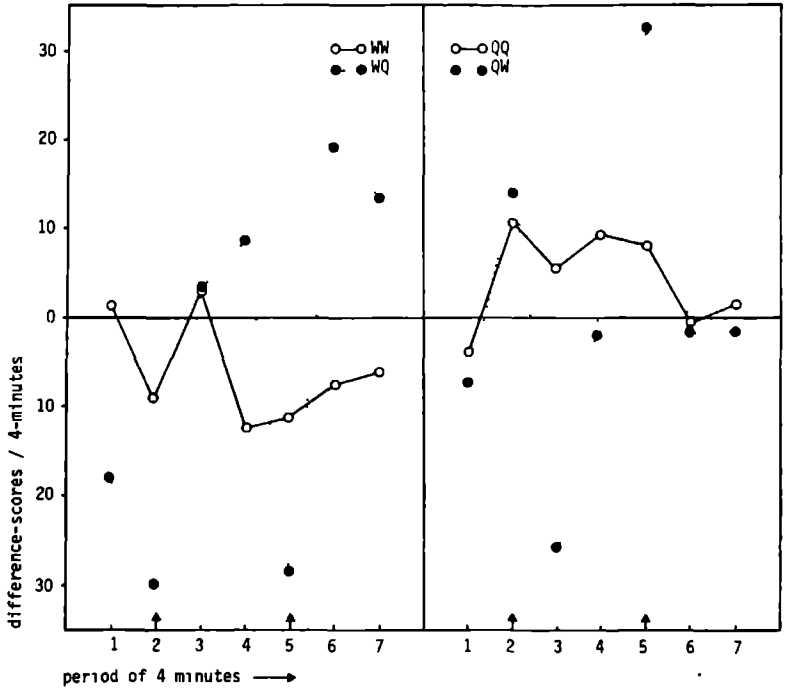


Figure 4.3. Mean difference-scores per period of 4 minutes. Difference-scores per period are computed by subtracting each subject's mean scores of the last 5 baseline sessions from each of its corresponding shift session scores. Shifts of reinforcement occur during the periods 2 and 5.

Because this decline obscured the picture of the shift effects, changes due to shifts were expressed in reference to individual baseline performance: scores were transformed into difference-scores, computed by subtracting each subject's mean of the last 5 baseline sessions from each of its shift session scores; this was done for each of the 7 response periods separately. All analyses were performed on these difference-scores. Figure 4.3 depicts the difference-scores for the four groups. Mutivariate

trend analyses were performed comparing each experimental group with its control group per period. Overall, subjects started their sessions with lower first period scores than during baseline training (multiv. F=5.20; df=1,19; p<.05), but this depressed response rate did not persist over the other periods.
Group WQ responded significantly less than group WW during both shift periods: in period 2 (multiv. F=16.74; df=1,19; p<.01) and in period 5 (multiv. F=9.70; df=1,19; p<.01). In addition, the graphically present positive contrast effect reached significance in both periods following the second shift: in period 6 (multiv. F=29.77; df=1,19; p<.01) and in period 7 (multiv. F=13.18; df=1,19; p<.01). In period 6 these groups differed also in trends (multiv. F=2.89; df=9,11; p<.01), which can be explained by the linear trend component: group WW showing no changes over days, group WQ slowly increasing.
In none of the 7 response periods did group QW differ significantly from group QQ. Thus, though graphically there were large shift effects in period 2 as well as 5, they did not reach statistical significance; neither were differences in postshift periods statistically present.

4.3. Experiment II. Water versus sucrose

The next experiment was undertaken to determine to what extent the changes reported in Experiment I can be generalized to shifts in the quality of reward when liquids are used that are more preferred than water. One suggestion for the appearance of positive contrast in Experiment I is, that the bitter taste of quinine causes the subject to drink more water after quinine presentations just to rinse its mouth, thereby reducing the elevated responding to a sensory after-effect, which for quinine is said to persist for more than an hour (Wong et al., 1970).
In contrast to Experiment I in which a reward was chosen which is clearly disliked by rats, in the present experiment a reward was used which is more preferred than water, i.e. a sucrose solution of 8%. One group of rats was exposed to shifts from water to sucrose rewards, whereas another group which had been trained on sucrose rewards was repeatedly shifted to water rewards. If a positive contrast will be found again, the positive contrast effect of Experiment I cannot be attributed merely to the purely perceptual after-effects of a bitter taste.

4.3.1. Material and Methods

Subjects and apparatus
Subjects were 24 experimentally naive male albino Wu rats (SPF63 Cpb) obtained from TNO, Zeist; they weighed about 310 grams at the start of the experiment. Treatment and apparatus used were essentially the same as those in Experiment I.

Procedure
The procedure followed was identical to that employed in the first study. Only the number of VI-30 sec baseline training sessions was reduced to 10, because in the previous experiment no substantial rate changes occurred after the 10th session.
An 8% sucrose solution (saccharose, weight/volume in tap water) was used instead of the quinine solution. A concentration of 8% was chosen because

it is known to produce intermediate rates of responding when compared with a variety of sucrose concentrations ranging from 4% to 32% (Weinstein, 1970a, 1970b). An intermediate level is prerequisite because of the possibility that at higher levels ceiling effects will obscure the development of positive contrast effects. Home cage intake of sucrose was measured on four non-training days.
Preceded by 10 CRF sessions, VI-30 sec baseline training continued for 10 sessions with group W receiving water as the reward and group S receiving the sucrose solution instead. During the shift phase of the experiment, the following groups, formed as before, were run: SW, SS, WS and WW, each group containing six subjects. The shift periods of each session were cued by a 1.000 Hz click tone as in Experiment I. Subjects were given 10 shift sessions.

4.3.2. Results

Sucrose intake in the home cage
Table 4.3 shows the amount of sucrose consumed during four 10-min presentations in the home cage. Although on the first day intake was relatively low, it was higher than the water intake in the reference group. The water group showed no further increases from the 2nd day onwards; the sucrose group, however, did. This resulted in a mean intake per day of 9.1 ml for the sucrose group and 7.4 ml for the water group.

Table 4.3. Group mean fluid intake (ml) during four 10-minutes presentations.

	WATER n=10		SUCROSE n=24	
DAYS	$\bar{X}$	SE	$\bar{X}$	SE
1	2.9	0.9	5.6	0.7
2	8.1	1.3	8.0	0.7
3	8.0	0.9	11.8	0.7
4	7.9	0.9	12.6	0.4

Baseline training
Mean response rates and standard errors of the means over the last 5 sessions of VI-30 sec training are shown in Table 4.4. The higher response rates of the sucrose group clearly reflect the higher incentive value of sucrose as compared to water. The number of reinforcements per day per group remained very stable, the sucrose group receiving about 7 more than the water group, presumably due to the different response rates. The steadily decreasing response rates within sessions found in Experiment I were also evident in this experiment.
On the data of the last 5 baseline sessions multivariate trend analyses were performed as before, comparing each experimental group with its control group per period of 4 minutes. Neither the groups SW and SS nor the groups WW and WS differed from each other in any of the seven 4-min periods.

Table 4.4. Mean response rates and mean reinforcement rates over the last 5 sessions of VI-30 sec baseline training. Rates were averaged per group per day.

	SUCROSE n=12		WATER n=12	
	$\bar{X}$	SE	$\bar{X}$	SE
Response rates	488	27.0	303	13.6
Reinforcement rates	44	0.9	37	0.6

As was to be expected from the foregoing experiment, in all periods except period 6 trends over days were apparent. The main part of these trends can be attributed to the oscillating rate increases of groups SW and SS respectively. These two groups do differ with respect to trends in period 1 (multiv. $F=5.74$; $df=4,17$; $p<.01$), period 3 (multiv. $F=3.34$; $df=4,17$; $p<.05$) and period 4 (multiv. $F=4.52$; $df=4,17$; $p<.05$). Group WS and WW do not differ at all in this respect.

Shifts in taste of reward

Response rates were averaged over individual subjects per period of 4 minutes and difference-scores were obtained as before (Figure 4.4). Multivariate trend analyses performed on these scores revealed significant overall effects in period 1 (multiv. $F=13.09$; $df=1,20$; $p<.01$), period 2 (multiv. $F=9.87$; $df=1,20$; $p<.01$) and period 3 (multiv. $F=14.37$; $df=1,20$; $p<.01$): all groups responded at a higher rate than during baseline training. In all periods, except period 7, significant trend effects were apparent (all $F>4.19$; $p<.05$). In all periods these effects are mainly accounted for by linear rate increases over days in group SS and group SW, the latter leveling off in the last days. These two groups differed significantly with respect to trends only in the periods 4 (multiv. $F=7.19$; $df=9,12$; $p<.01$) and 5 (multiv. $F=3.27$; $df=9,12$; $p<.05$).

A complication arose in the appearance of a substantial overall difference between group WS and its control group WW in period 1 (multiv. $F=6.65$; $df=1,20$; $p<.05$): before any experimental intervention had been made group WW responded at a higher rate than group WS. It is difficult to say what aspect of the situation accounts for this effect. However, its occurrence hinders the comparison between both groups with respect to the appearance (or nonappearance) of effects due to shifts in reinforcer. Therefore, an analysis of covariance was performed on the data, aimed to statistically correct for these initial differences, using period 1 as a covariate.

With respect to shift and postshift effects: in period 2 no shift effects were evident, neither group SW nor group WS differing from its respective control group. Group SW responded at a significant lower rate than group SS in period 5 (multiv. $F=4.61$; $df=1,19$; $p<.05$) and group WS responded at a higher rate than group WW in the same period (multiv. $F=15.61$; $df=1,19$; $p<.01$), i.e. both groups changed their performance in accordance with the direction of the reward shifts.

Group SW responded at a significant higher rate than group SS in period 3 (multiv. $F=4.40$; $df=1,19$; $p<.05$) and in period 6 (multiv. $F=5.16$; $df=1,19$; $p<.05$), whereas in the period 4 and 7 significance was approached

(p<.06 in both cases). Nowhere in the postshift periods did group WS differ from group WW.

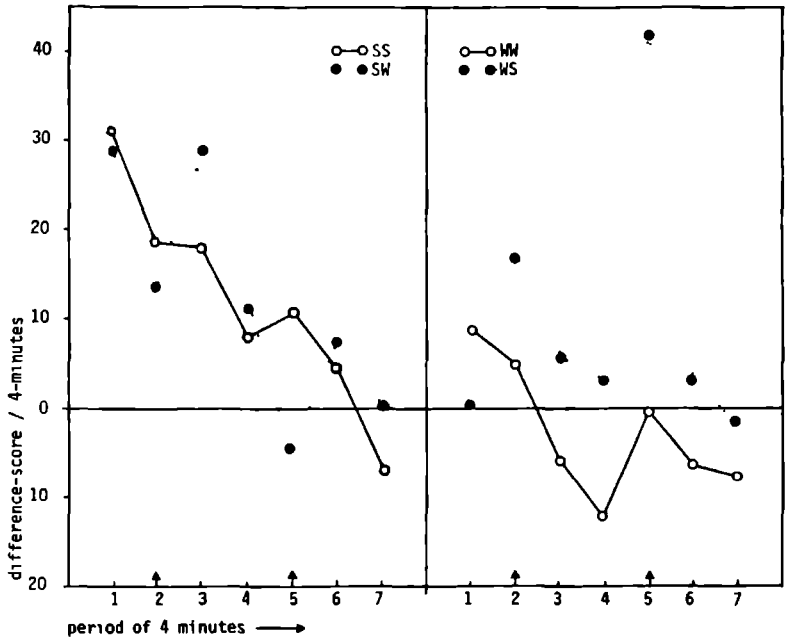


Figure 4.4. Mean difference-scores per period of 4 minutes. Difference-scores are computed by subtracting each subject's mean scores of the last 5 baseline sessions from each of its corresponding shift session scores. Shifts of reinforcement occur during the periods 2 and 5.

Because of the afore-mentioned trend effects (in all but the seventh period), an analysis of covariance was performed on the data of the last 5 shift sessions, with period 1 as a covariate. The results for the groups SS and SW changed only in so far that group SW's higher response rates reached significance in period 4 also (multiv. F=6.69; df=1,19; p<.05). More surprisingly, group WS responded at higher rates than did group WW in period 6 (multiv. F=4.63; df=1,19; p<.05) and reached almost significance in period 4 (p<.07), therewith demonstrating positive induction effects.

4.4. Discussion

4.4.1. Quinine and sucrose intake in the home cage

The very low scores of both the water and the quinine groups (Experiment I) on the first day probably represent an effect of unfamiliarity with the measuring procedure per se which, of course, is the same for both groups. The same can be said of the sucrose group (Experiment II) which on the first day also scores much lower than later on. The leveling off in the water group from the second day onwards, in contrast to the further increases in the quinine group on a lower level, and in the sucrose group on a higher level than the water group, suggests that the later leveling off in both taste groups may be due to a flavour neophobia which becomes attenuated as subjects become more familiar with the solution and which, of course, is absent in the water group. The relative preference for all three substances, however, is clearly demonstrated on all days.

4.4.2. Baseline training

The differential response levels of group Q and group W in Experiment I and group W and group S in Experiment II are consistent with the general incentive effects of differences in reward quality on instrumental performance (e.g. Pfaffman, 1961; Bolles, 1975a; Rashotte, 1979a). In contrast, the declining response rates within sessions we continuously found are incontestably not in line with the common reports of steady response rates obtained from VI schedules (e.g. Mackintosh, 1974b; Pear and Wilkie, 1971; Nevin, 1973), though it is also sometimes reported that operant responding on an interval schedule for water is less stable than for food (Ferster and Skinner, 1957; Terrace, 1968). Petrinovitch and Bolles (1954) suggested that in a natural environment rats are searching for food almost continuously, but have at their disposal a comparatively constant supply of water. Maybe, that is why operant behaviour shows more persistency for food than for water.
The most obvious explanation seems to be that the declining rates are caused by satiation effects. However, rates are already declining considerably in period 3, that is, after 8-12 minutes of responding. In this period of time subjects have received twenty rewards at the most, or maximally 2 ml of fluid. This amount seems too small to be able to cause satiation effects. True enough, Goodson et al. (1962) report that drinking rates in a free drinking test decrease gradually; inspection of their data, however, reveals that water consumption starts to slow down only after an almost steady intake of 5-7 ml. We found the same in a pilot study. The total amount of fluid which a subject obtained per session in the experiments reported here does not exceed 3.5-4.5 ml. Therefore, satiation cannot be considered an acceptable explanation for the declining response rates which were observed. This, of course, does not exclude the possibility that the relatively large volume per reinforcement (.1 ml) played a part in the declining response rates.
Another possible interpretation might be that the animals anticipated the one hour water presentation following completion of the test session. This would be in accordance with the data showing that, in multiple schedule tests, the following schedule may influence behaviour at least as much as the preceding schedule (Wilton and Gay, 1969; Williams, 1976a, 1979, 1981; Checke, 1982). There are some data indicating that home cage feeding conditions may influence behaviour in the experimental apparatus (Bacotti, 1976). However, to my knowledge no studies demonstrate a similar effect of the daily water ration, when given immediately following the tests, upon performance in the test.

4.4.3. Shifts in the taste of the reward

Before discussing effects due to shifts in reward, overall response rates during the shift sessions have to be considered. In Experiment I 22 training sessions were presented. Because in the first experiment rates did in fact not substantially change any more after the tenth training session, subjects in Experiment II were given 10 VI-30 sec training sessions only. Several lines of evidence indicate that this has been too few. First, trend analyses on the data of the shift sessions revealed significant overall effects in the first three periods of each session, response rates during shift sessions being consistently higher than before. Secondly, in all periods except the seventh, significant trend effects brought out rate increases over days. Thirdly, inspection of individual data showed a great many subjects to respond at higher levels during shift sessions than during baseline training. This is in accordance with reports that barpress performance on a VI schedule does not stabilize until after 15-20 sessions (Mackintosh, 1974b). The continuing rate increases are particularly evident in groups SS and SW. It is not clear whether they are caused by sucrose being the reward in these groups. Differences in incentives are not usually thought to affect rate of acquisition, though their influences upon asymptotic performance are well documented (Bolles, 1975a) and are shown here too. However, sometimes they fail to produce different asymptotes, while still yielding different response levels during acquisition. In a number of studies by McCain et al. (1971) large rewards produced better performance during acquisition, but the small reward groups finally catched up and differences had disappeared when asymptotic levels had been reached. In our case, what happens seems altogether different: it is the sucrose groups, SS and SW, that keep raising their rates and it is the water groups, WW ad WS, that seem already relatively close to asymptote. Thus, differences seem to increase rather than to disappear. Whether this may be due to the fact that we varied quality rather than amount, is not clear.
Because shift and postshift effects were evaluated by means of group comparisons, increasing response rates are no hindrance to the interpretation of the results due to shifting the quality of reward: the groups to be compared showed the same tendencies.

In both experiments reported here positive contrast effects have been demonstrated, whereas negative contrast effects did not show up at all. As for the first experiment, it might be suggested that perhaps the subjects shifted to quinine did not consume all reinforcers obtained and that their positive contrast effect merely reflects increased thirst. However, it has been observed elsewhere that even with much stronger quinine solutions, rats do consume all reinforcers, be it quinine adulterated water be it quinine adulterated food (Oakley, 1975).
A possible explanation in terms of sensory after-effects caused by the bitter taste of quinine can be ruled out also, because a pilot study revealed that after the ingestion of 1 ml of quinine rats do not consume more water than after an intake of 1 ml of water. Moreover, in the second experiment, using sucrose as the reward, essentially the same effects were obtained: whether quinine versus water rewards or water versus sucrose rewards were employed did not affect the outcome. Therefore, both objections that perhaps subjects did not consume all quinine rewards and that subjects tried to get rid of a bitter taste by drinking more water, can be safely rejected.

The finding of positive but not negative contrast is rather curious in the light of the fact that in rats the positive contrast effect has been proven to be much more elusive than the ubiquitous negative contrast effect. However, most experiments that substantiated this pattern of results have been employing the simultaneous contrast design, utilizing discrete trial runway situations. For example, using different concentrations of sucrose, Flaherty et al. (1973a) convincingly demonstrated a simultaneous negative contrast effect, without being able to demonstrate the occurrence of a positive contrast effect.
Until recently, in critical reviews of the contrast literature positive contrast effects in rats have been considered nonexistent and the few studies that did report its occurrence have been put aside on grounds of procedural imperfection (Dunham, 1968; Black, 1968; Mackintosh, 1974b). A number of recent investigations, however, has demonstrated positive contrast effects in rats in a variety of situations (Baltzer and Weiskrantz, 1970; Beninger, 1972; Flaherty and Avdzej, 1974; Allen and Porter, 1975; Shanab and Cavallaro, 1975; Flaherty and Lombardi, 1977; Porter and Allen, 1977; Flaherty et al., 1977, 1979b; Boyer and Swank, 1980).
On the other hand, experiments employing pigeons in free operant behavioural contrast tests reliably produce the behavioural positive contrast effect (e.g. Pear and Wilkie, 1971; Wilkie, 1977). Our results obtained with rats in a free operant situation are clearly in keeping with this latter evidence, as far as the occurrence of the positive contrast effect is concerned (Gutman et al., 1975; Beninger and Kendall, 1976; Gutman, 1977a, 1977b; McSweeney, 1982).
Especially pertinent to our study are the results obtained by Flaherty e.s. who, varying the concentration of the sucrose reward, were able to demonstrate positive contrast effects, and ,contrary to our results, negative contrast effects as well (Flaherty and Avdzej, 1974; Flaherty and Largen, 1975; Flaherty and Lombardi, 1977). In these experiments, however, consummatory rather than instrumental responses (lick rate) were measured. With other responses positive contrast effects are still not found widely in the simultaneous contrast experiment, unless special steps are taken (Bower, 1961; Chechile and Fowler, 1973; McHewitt, 1974; Calef et al., 1975; Shanab and Kong, 1977; see also chapter II, section 2.3.2).

Negative contrast effects have been demonstrated in numerous studies employing simultaneous contrast designs (Black, 1968; Dunham, 1968; Mackintosh, 1974b; Rashotte, 1979b; Flaherty, 1982). In behavioural contrast studies designed to detect a negative contrast effect it has been demonstrated, with pigeons as well as with rats (e.g. Brownlee and Bitterman, 1968; Wookey and Strongman, 1971; Schwartz, 1975; McSweeney, 1982). Therefore, although it is somewhat surprising that a positive contrast effect was found by employing shifts in the palatability of the reward, it is much more puzzling that no negative contrast effect was observed at all. Its occurrence may have partly been masked by a floor effect, especially in the periods after the second shift where rather low response rates were obtained; the absence of even the slightest tendency to a negative contrast effect following the first shift can not be explained that way.
Another possibility is that there are genuine individual differences in the tendencies of rats to show negative contrast effects (Pear and Wilkie, 1971; Poli and Motta, 1979). Therefore, the individual data were inspected to clarify the picture. One-tailed t-tests were performed per

subject, comparing the last 5 baseline sessions with the 10 shift sessions. It was revealed that the groups devised to demonstrate negative contrast effects (group QW in Experiment I and group WS in Experiment II) both showed considerable individual differences in postshift responding, whereas both other experimental groups (group WQ in Experiment I and group SW in Experiment II) behaved rather uniformly. In any case, the individual variation in these groups appeared not to be related with differences in motivational level, as measured by response rate ($r=.72$; $p>.05$ in Experiment I and $r=.42$; $p>.05$ in Experiment II; Spearman Rank Correlation Coefficient, Siegel, 1956); nor was a relation found with deprivation level, as expressed in percentage weight loss at the time of testing ($r=.62$; $p>.05$).

The precise values of experimental parameters are obviously important. It is not clear why the negative contrast effect would be more sensitive to its influences. This would be contrary to the report of Baltzer and Weiskrantz (1970) who showed the positive contrast effect to be the more sensitive to variations in several parameters, such as reinforcement density, schedule requirements, amount of reward changes, and employment of liquid instead of food rewards, whereas the negative contrast effect was totally unaffected. This is the pattern that was to be expected as a consequence of the many reports concerning reliable NCE's as opposed to the scarcity of demonstrations of positive contrast effects.

Finally, it is clearly shown that the occurrence of reliable shift effects does not necessarily result in contrast effects also, and conversely, that reliable contrast effects do not require prior shift effects to occur.

CHAPTER V

SHIFTS IN QUALITY VERSUS SHIFTS IN AMOUNT OF REWARD

The previous experiment examined upshifts and downshifts in palatability of liquid rewards in two analogous free operant experiments. Reliable positive contrast effects were obtained but no indications of negative contrast effects. Because these results are rather atypical for experiments utilizing rats, an attempt will be made to assess the generality of these findings. Purpose of the present study is to replicate the results obtained in the foregoing experiments with shifts in the quality (palatability) of the rewards and to extend them to shifts in a different parameter of reinforcement.
One possible explanation for the absence of the otherwise well documented negative contrast effect may be the fact that in experiments that consistently produced the negative contrast effect, amount of reward is usually varied rather than quality (Cox, 1975; Rashotte, 1979b; Flaherty, 1982). Therefore, it was aimed to examine the effects of shifting the amount of reward. This was done by offering various groups a larger reward during shifts, a smaller reward, or no reward at all. The nonreward condition closely resembles free operant studies utilizing multiple schedules, one component of which is extinguished. The often tacit assumption is that this reduction in the amount of reward to a zero value is essentially equivalent to reductions from large to small rewards (Reynolds, 1961a; McHose and Moore, 1976; Shanab and Gersh, 1976; Gutman, 1977b; Pingrey et al., 1979).

5.1. Material

Subjects
Subjects were 60 experimentally naive male albino Wu rats (SPF63 Cpb, Loosli, 1975), obtained from TNO, Zeist. At the start of the experiment they weighed approximately 350 g. All animals were housed individually in Macrolon cages and received food ad lib. They were stocked in a room adjacent to the experimental room. All testing was done in the dark period of their reversed day/night schedule.
From the 60 rats originally entering the experiment only 47 completed the experiment: some subjects were discarded because they learned the barpress response too slowly and fell too far behind the others; some others were removed because of either extremely high or extremely low response rates, which hampered the splitting up of subjects into seven equal groups.

Apparatus
Eight identical experimental chambers manufactured by Campden (model 410) were used. They were modified so that there was only one retractable lever near the frontwall of the box. A force of 8 g was required to activate the lever. A recess in the centre of the wall gave access to the reinforcer: the liquid reward was delivered up to the floor of the recess by a motor operated dipper. The dipper remained in the up-position for 6 seconds per reinforcement. Dipper volumes used were .05 ml for the standard condition and either .1 ml or .02 ml for the shifted conditions. Dipper presentations were signaled with lighting of the recess. Each chamber contained four additional lamps: one was located above the lever and

another at a corresponding position at the far side of the same wall; a third light was placed above the recess and a houselight was located on the ceiling. While the houselight remained on during sessions, the other, lights flickering in unison, served to signal the shift period. During time-out periods the lever was retracted and the houselight was switched off.
Each chamber was enclosed in a sound attenuating cubicle; its frontwall was left open to facilitate within-session changes in reward. An exhaust fan ventilated the chambers and provided constant masking noise. Scheduling of experimental events and data collection were accomplished with a Digital Equipment Corporation PDP 11/03 computer located in the same room. The room was dimly illuminated by a red light.

5.2. Procedure

Baseline training and quinine/sucrose intake
Following several days of adaptation to a water deprivation schedule of 22 1/2 hr, subjects were shaped and trained to barpress for .05 ml of water on a continuous reinforcement schedule. At the end of each 15-minutes training session they received water in their home cages for an hour. After 10 sessions of CRF training the schedule was changed into an randomized VI-30 seconds schedule. Sessions were lengthened to 24 minutes and divided into 5 periods of 4 minutes each, separated by a 1-minute time-out. During the time-out the houselight was switched off and the lever was retracted.
After 10 sessions of VI-30 sec training, four 15-minutes sessions of FR-5 were inserted to raise the response rates, which until then were rather low. Following this, 12 VI-30 sec sessions were given as before. At this stage subjects were assigned to one of seven groups. Some rats had to be discarded because of extreme scores, as mentioned before.
Following baseline training, on three consecutive nontraining days groups WQ and WS (see below) were given 15-minutes presentations of a quinine solution (.01% QHCL, weight/volume in tap water) or a sucrose solution (8% saccharose, weight/volume in tap water) respectively, in their home cages. Amount consumed was recorded. This was done in order to eliminate possibly interfering neophobia effects later on in the experiment and to ascertain that each subject of the respective groups did in fact consume the concentration employed.

Shifts
The following groups were formed:
- WQ (n=7), receiving a .05 ml volume of the quinine solution as the reward during the shift period;
- WS (n=7), receiving a .05 ml volume of the sucrose solution during shifts;
- W.1 (n=7), receiving a .1 ml volume of water reward instead of the standard .05 ml during shifts;
- W.02 (n=7), receiving a smaller volume of .02 ml of water during shifts;
- WE (n=6), being exposed to extinction during shifts in that dipper presentations continued without the dipper containing any reward;
- and WW (n=7), the control group that received the standard .05 ml volume of water during shifts.
- EW (n=6), the seventh group, was exposed to a rather unusual procedure, in that during the normal nonshift periods nonreward, i.e. extinction was

in effect and dippers didn't contain any fluid, whereas during shifts a reward of .05 ml of water was given.
The 24-minutes sessions were divided in 5 periods of 4 minutes each, separated by 1-minute time-outs (Figure 5.1). Shifts in the reward were effectuated during the third period; thus, each shift was preceded as well as followed by two standard periods. The shifts were cued by a flickering-in-unison of all four lamps in the experimental chamber for the full 4 minutes the shifts were in effect. All subjects were given 10 shift sessions on 10 consecutive days.

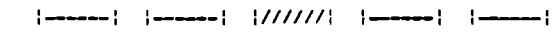


Figure 5.1. Graphic representation of a shift session.

5.3. Results

Quinine and sucrose intake
On three consecutive days volumes of quinine and sucrose respectively consumed during 15-minutes presentations in the homecage were recorded. Results are shown in Table 5.1.

Table 5.1. Quinine and sucrose consumption in the home cage (in ml).

DAY	QUININE n=7	SUCROSE n=7
1	1.1	6.8
2	2.3	12.7
3	2.4	12.4

These results are almost identical with the results obtained in the earlier experiments (Chapter IV). On that occasion, consumption of tap water fluctuated around an 8 ml volume.

Baseline training
Because the overall response rates (after 10 sessions of VI-30 sec training) were rather low, a few FR-5 sessions were interpolated. After these an additional 12 VI-30 sec sessions were given. Response rates during the last 5 baseline sessions averaged 310 responses per session. Within a session, a decline in rate of responding occurred from approximately 85 responses during period 1 to some 30 responses during period 5. Due to sessions being shortened by two periods rates did not fall as low as in the previous experiment. Almost all reinforcers available in the last period were obtained.
After groups were formed, training data were considered per group. Table 5.2 summarizes mean response rates and standard errors of the means over the last 5 days of baseline training. Group EW was excluded from analysis because its peculiar treatment later on in the experiment rendered it quite uncomparable to the other groups.

Table 5.2. Mean response rates over the last 5 sessions of VI-30 sec baseline training.

	WW n=7	WS n=7	WQ n=7	WE n=6	W.1 n=7	W.02 n=7
$\bar{X}$	310	297	323	310	320	313
SE	9.8	11.4	16.4	24.0	23.7	10.5

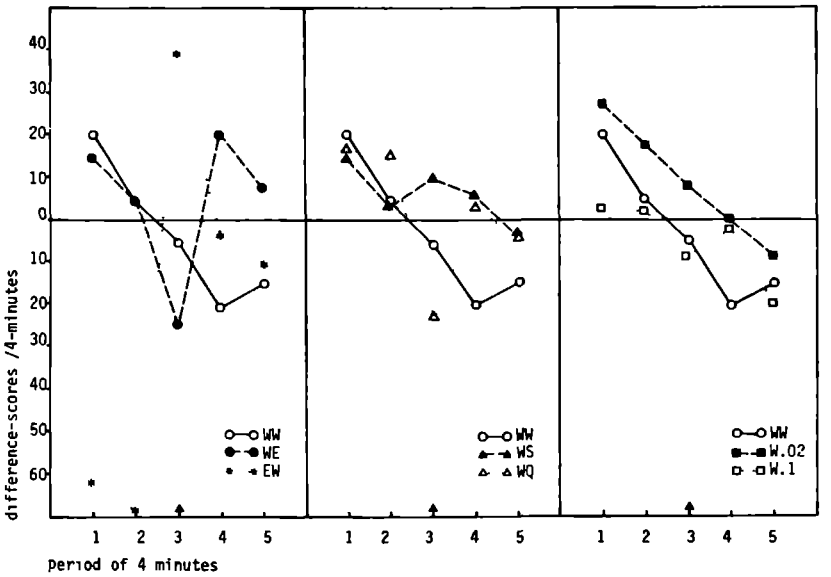


Figure 5.2. Mean difference-scores per 4 minutes. Difference-scores are computed per period by subtracting each subject's mean scores of the last 5 baseline sessions from each of its corresponding shift session scores. Each panel shows the control group with two opposite experimental groups. The arrow indicates the period containing the shift of reinforcement.

Multivariate trend analyses (Finn, 1977) were performed on the data of the last 5 baseline sessions, in which each experimental group was compared with control group WW for each period separately. None of the experimental groups differed significantly from group WW during any of the periods.

Trends were apparent during the period 1 (multiv. F=2.94; df=4,32; p<.05), period 3 (multiv. F=9.86; df=4,32; p<.01) and period 5 (multiv. F=4.63; df=4,32; p<.01). These effects, however, appeared to be rather random and probably do not represent genuine effects. The experimental groups did not differ from group WW in this respect, except group W.1 which showed less stable response rates than group WW over the last 5 sessions in period 5 (multiv. F=5.92; df=4,32; p<.01).

Shifts in reward

Response rates per 4 minutes were transformed into difference-scores by subtracting a subject's mean of the last 5 baseline sessions from each of its shift sessions. Figure 5.2 shows mean difference-scores per group. All analyses were performed on these difference-scores. Multivariate trend analyses compared each experimental group with control group WW.

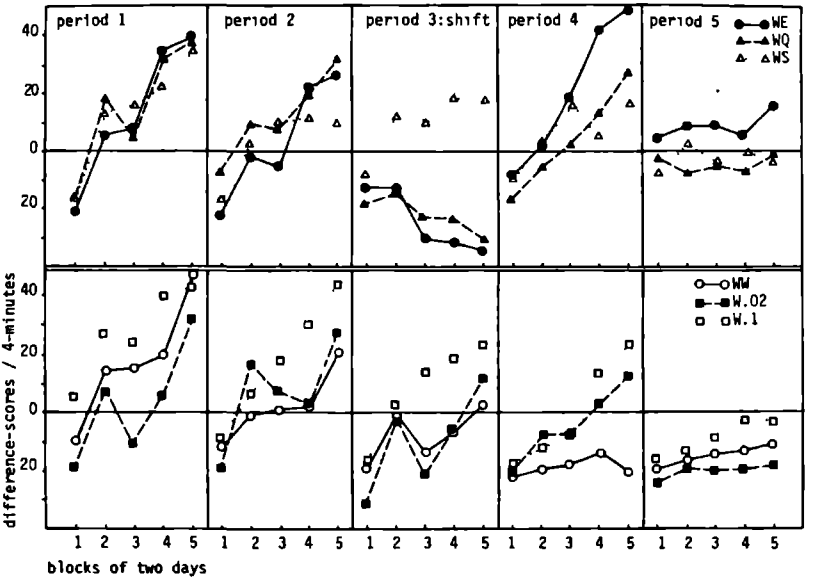


Figure 5.3. Difference-scores shown for each period separately. Difference-scores are computed by subtracting each subject's mean scores of the last 5 training sessions from its corresponding shift session scores. Difference-scores have been averaged per two days. The upper series of graphs shows the groups WE, WQ and WS; the lower series shows the groups WW, W.02 and W.1.

Overall, subjects started their sessions with higher scores than during training in period 1 (multiv. F=18.26; df=1,35; p<.01) and period 2

(p<.06). In period 3, however, rates were significantly lower, due to shift effects (multiv. F=5.06; df=1,35; p<.05). In all periods, (linear) increases in responding were found; for all periods multiv. F>7.10; df=9,27; p<.01 (see also Figure 5.3).
Rate differences between experimental groups and control group WW were absent in the first two periods and only once did an experimental group show different trend effects than group WW: group W.1 showed more rate oscillations over days in period 2 (multiv. F=2.55; df=9,27; p<.05).
In period 3 shift effects were apparent: group WS responded significantly more than group WW (multiv. F=5.69; df=1,35; p<.05); group WQ responded less and approached significance (p<.06) and group WE responded less (multiv. F=5.19; df=1,35; p<.05) when compared with group WW. Group WE also showed trend differences (multiv. F=4.23; df=9,27; p<.01): its response depression became stronger over days. Groups W.1 and W.02 did not differ from group WW.
In postshift period 4, group WE showed a reliable positive contrast effect in responding at a significantly higher rate than group WW (multiv. F=4.49; df=1,35; p<.05); group WQ approached significance (p<.07), and group W.02 did not show any effect. None of the other groups differed from group WW and whereas linear increases were apparent, as described above, no trend differences were found.
In postshift period 5 no effects were found.
As mentioned before, group EW was quite incomparable to any group, mainly because its pre- and postshift responding could not be evaluated against another group's performance. Nevertheless, during shift period 3 its performance can be evaluated and the results are interesting: with group WW serving as a reference and both groups receiving identical rewards, group EW responded at a considerably higher rate than did group WW, therewith demonstrating a positive contrast effect as a consequence of the preceding extinction condition in the periods 1 and 2.

5.4. Conclusions and discussion

As for the quinine/sucrose intake in the homecage essentially the same was found as in the previous experiments. Rats did consume the concentrations used, though level of intake clearly reflected relative preference.
During baseline training as well as during the shift phase of the experiment a persistent within-session decline of responding occurred. Compared with the previous experiments the reward volume was reduced from .1 ml to .05 ml. Therefore, an explanation of this decline in terms of satiation effects seems even less likely than before. True enough, in the present experiment rate of responding declined less than before. This seems to result from shortening of the session's duration with two periods rather than from a reduction in reward volume. Moreover, even though reward volume was halved, response rates during the last period of the present experiment were quite comparable with those of the fifth period of the previous experiments (about 30 responses per 4 minutes). The possibility of interference from floor effects in post shift periods has herewith receded as well; in the previous studies subjects were quite capable of significantly undershooting the response level of this fifth period during negative shifts of reward.
Overall rates of responding fell below baseline level on the first two shift sessions. This was apparent in response scores per period as well. This was probably caused by a pause of three days interspersed between the

training and shift phase of the experiment. During the third shift session performance recovered. Whereas in the previous experiments 10 sessions of baseline training had proven to be too few for establishing stable response levels over sessions, 22 had seemed quite enough (see also Mackintosh, 1974b). Yet, after 22 sessions of baseline training response rates in the present experiment kept rising for all groups alike. This was revealed by the occurrence of significant trend effects in all periods. And, as before, the continuing increase in responding was most prominent in the first and second periods of each session.

The principal results due to manipulations of the reward were the following: both groups WS and WQ and both groups WE and EW changed their performance in accordance with the direction of the shifts in reward. Shifts in amount of reward (group W.1 and group W.02) did produce no such changes. The latter result is remarkable as -at least with food as the reward- amount of reward is generally considered a very important determinant of strength of motivation (e.g. Mackintosh, 1974b; Bolles, 1975a; Beck, 1978; Rashotte, 1979a). And particularly VI schedules are thought to be extremely sensitive to changes in the level of motivation (Pfaffman, 1961; Bolles, 1975a; Rashotte, 1979a).

In post shift period 4 positive contrast effects have been found in the groups WQ and WE; group WS did not show the slightest tendency to negative contrast effects. And again, group W.02 and W.1 were not affected by the reward variations. This demonstration of positive contrast effects concomittant with a glaring absence of a negative contrast effect replicates and extends our previous findings to situations involving extinction of one component.

The one situation almost always producing positive contrast effects in pigeons as well as in rats is the behavioural contrast paradigm. Employing free operant situations and extinguishing one component of a multiple schedule, contrasts are expressed in terms of changes of subjects' rates of responding in the unchanged schedule component, as the result of these schedule differences (Dunham, 1968; Freeman, 1971; Cox, 1975; Williams, 1983). Positive contrast effects after shifts in the quality of reward have not been reported in this paradigm. Conversely, in the simultaneous contrast design, utilizing rats, the positive contrast effect is not always found. Our demonstration of a positive contrast effect due to nonreward as well as a shift in the quality (palatability) of reward in a design that cuts across the behavioural/simultaneous distinction might be an indication of a larger generality of the positive contrast effect than is normally assumed.

Another important aspect of the results is the localization of the contrast effects in the period immediately following the shift (Mackintosh, 1974b; Rashotte, 1979b; Williams, 1983). This is reminiscent of the local variety of the behavioural contrast effects, even though our time-scales differ. It is important to note in this context, that precisely the local contrast effects show the clearest symmetry.

The conditions producing the positive contrast effect in group WE seem to be more compelling than those producing the effect in group WQ, as can be seen in the much stronger shift as well as contrast effects occurring in the former group. Basically, however, these groups demonstrate an identical pattern of behaviour. This conclusion does not apply to group W.02 that showed hardly any effects at all. It may be that the differences between the two reward sizes were not large enough for rats to be perceived. It is well known that the size of contrast effects increases when the reward disparity is larger (e.g. Flaherty, 1982). Since we found

positive contrast effects the difference between the two reward sizes should have been large enough; in many studies variations of magnitude of the reward did not produce positive contrast effects (Shettleworth and Nevin, 1965; Kramer and Rilling, 1969; Mackintosh et al., 1972; Mackintosh, 1974b). These studies all suggest that the occurrence of a small reward in a situation associated with a larger reward may not be sufficient to produce a positive contrast effect. Also related is the finding of Mackintosh et al. (1972) that a positive contrast effect was only observed when the changed component of a multiple schedule was correlated with a lower probability of reinforcement than in the unchanged component; it was not found when it signalled equally probable but smaller rewards. The assumption often made implicitly in many contrast studies that a procedure employing extinction during one component is merely a special instance of the more general contrast paradigm varying amount of reward, thereby seems invalid. Unfortunately, by my knowledge no study has plotted the occurrence of contrast effects over a whole range of reward magnitudes, including a zero magnitude.

Our failure to obtain negative contrast effects corroborates our earlier findings. It cannot be attributed to limiting floor effects, as has been shown. Moreover, if anything, induction appeared to result from the shifts in a positive direction. The finding that, in period 4, group WS did not differ from group WQ which showed a strong tendency towards positive contrast effects, points to the same conclusion. Though this may be accepted without too much puzzlement for group WS, the absence of a negative contrast effect in group W.1 is rather curious. The consistently found negative contrast effect in discrete trial situations utilizing runways, is in fact produced mainly by varying magnitude of reward (e.g. Black, 1968; Cox, 1975; Flaherty, 1982). Individual differences might account for our second failure to demonstrate negative contrast effects in group W.1 and WS, as it did in our previous experiments (see Chapter IV). One-tailed t-tests comparing the 10 shift sessions with the last 5 baseline sessions revealed that, typically, subjects in positive contrast groups (WQ and WE, but not W.02) behaved very uniformly, whereas the negative contrast groups (WS and W.1), plus W.02, were remarkably dishomogeneous. This dishomogeneity was not related with deprivation level, as measured through percentage weight loss ($r=-.38$ and $r=.00$ respectively; $p>.05$; Spearman Rank Correlation Coefficient, Siegel, 1956); nor was it related with drive level, as measured through absolute rate of responding ($r=.58$ and $r=-.65$ respectively).

Taken together, the results point to the following:

- changes in palatability of the reward did produce a positive but not a negative contrast effect, as found before;
- varying amount of reward was not sufficient to produce either a positive or a negative contrast effect in a free operant situation, though according to the literature it may do so in a discrete trial runway situation;
- omission of reward produced the strongest positive contrast effect and appears not to be related to other shifts in amount of reward.
- the occurrence of shift effects is not necessarily followed by contrast effects; and contrast effects can occur without being preceded by shift effects.

CHAPTER VI

CONTRAST EFFECTS IN RATS RUNNING FOR LIQUID OR SOLID REWARDS

6.1. Introduction

Behavioural effects of transitions from one reinforcer to another (and back) have been extensively investigated in a variety of differential conditioning situations (Mackintosh, 1974b; Rashotte, 1979b; Flaherty, 1982). These studies were aimed at throwing some light upon the mechanisms determining the different behaviour patterns induced by contrasting conditions of reinforcement. Roughly speaking, the data fall into two categories. In free operant situations utilizing multiple schedules, positive behavioural contrast effects are reliable phenomena when pigeons are used, but they are much less commonly found with rats. Negative contrast effects, on the other hand, are easily demonstrated by employing rats in the discrete trial runway situation (simultaneous procedure), in which size of the reinforcer is the parameter varied .

In a series of previous experiments (Chapter IV and V) we have tried to reconcile the two sets of data by placing rats in a free operant situation and varying either amount or quality/palatability of the reward, in order to induce the positive contrast effects in rats and, of course, the more common negative contrast effects as well. Positive contrast effects were found together with a glaring absence of negative contrast effects, when quality of reward was shifted. When reward was alternated with extinction, the strongest positive contrast effects were found. When amount of reward was varied, no changes in behaviour were seen at all.

As has been elaborated elsewhere (Chapter II and III) the behavioural contrast (free operant leverpress) experiments on the one hand and the simultaneous contrast (discrete trial runway) studies on the other hand do differ considerably on a number of presumably important aspects. Though the most conspicious of these, the species difference (pigeons versus rats) does not seem to contribute to the discrepancy of the general pattern of results.

Procedural differences might be more important. For example, the response required for pigeons is usually the keypeck, a response considered topographically very close to the consummatory response, whereas the response required in alleyways is running, which seems relatively far removed from the final consummatory response (Snyder and Hulse, 1961; Shapiro and Miller, 1965; Schwartz and Williams, 1972; Allison, 1976; Pfaffman, 1982). Even though the leverpress response of rats is not necessarily topographically similar to the keypeck response of pigeons (Mackintosh, 1974b; Flaherty and Caprio, 1976; Bouzas, 1976; Bouzas and Baum, 1976; Young and Black, 1977), positive contrast effects can be obtained with rats pressing the lever (see Chapter II, section 2.3.3; see also Chapter IV and V).

Rate measures on one hand and speed or latency measures on the other might well be differently sensitive to motivational changes (e.g. Traupman and Wong, 1971; Mackintosh, 1974a; Bolles, 1975b). And finally, different measures set different boundaries to performance changes: with latency/speed measures performance improvement will be limited by physiological boundaries, whereas there is ample room for performance deterioration; with rate as the measure upper limits to performance

improvement can be shifted by adapting schedule requirements, whereas there is no correction possible for floor effects.
The studies to be reported here aim to explore the generalizability of the results from the previous free operant tasks in the discrete trial runway situation, which is the test situation commonly employed with rats. The length of the runway we will employ, the many turns and the hurdles placed in the alleys all serve the goal of decreasing running speed, for the danger of rats running too fast is very real (cf. ceiling effects, see Chapter II, section 2.3.2). In a pilot study it was attempted to slow down the subject's running by inserting a 10-sec delay between arrival in the goalbox and presentation of the reward. However, this manipulation did not affect running times at all. As we were using liquid rewards at that time, this finding might well be related to the reports that delay of water reward has a much slighter effect on performance than does an equivalent delay of food (Logan and Spanier, 1970). Therefore, the delay was relinguished again.

6.2. Experiment I. The effects of changes in liquid rewards

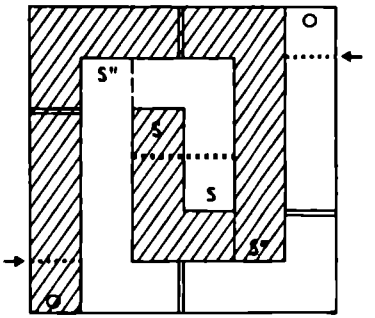
The first experiment to be reported used liquid rewards. Special care was taken to design the present experiment so as to match as closely as possible the former free operant experiments. Thus, quality was varied by offering an 8% sucrose solution or an .01% quinine solution. Varying amount of reward is the one technique that almost invariably produces negative contrast effects with rats (Black, 1968; Dunham, 1968; Mackintosh, 1974b; Rashotte, 1979b; Flaherty, 1982). In our study the amounts were chosen such as to equalize amount consumed per block of trials with the amount consumed per 4-minutes period in the free operant tasks (described in Chapter IV and V). It has often been stated that speed of running in an alley reliably reflects motivational differences: it increases if reward size increases (e.g. Gonzalez and Bitterman, 1969: Wike and Chen, 1971; Daly, 1972), if volume of water reward increases (Kintsch, 1962) and if concentration of sucrose solution increases (Goodrich, 1960; Kraeling, 1961; Snyder, 1962; Rosen, 1966).

6.2.1. Material

Subjects
As subjects served 50 naive male Wu rats (SPF63 Cpb; Loosli, 1975), obtained from TNO, Zeist. At the start of the experiment they weighed an average of 190 g ($\pm$ 10). They were housed individually in Macrolon cages and stocked in a room adjacent to the experimental room under reversed day/night conditions. All testing took place during the dark period. Each subject received its daily 1-hour ration of water immediately following its last trial. In all phases, subjects had free access to food. From the 50 rats originally entering the experiment 17 were discarded because they either did not learn the required response due to excessive freezing behaviour, or did not consume the rewards offered.

Apparatus
The apparatus was a square wooden box with hinged, clear plexiglas,covers. It was adapted to form two "circular" runways (see figure 6.1). The floor and walls of one runway were painted black, those of the other were painted

white. The start compartments were located in the centre of the apparatus and rats had to run an anticlockwise "circle" to reach the goal compartments. Width and height of the alleys were 16 cms. Total distance from start to goal compartments was 265 cms. Start doors were operated manually and recording of running time was done by means of a stopwatch. The many turns in the runway were meant to lower the very fast running times, as were the two hurdles of 6 cm height placed in each alley.



S startbox with hinged door
... hinged door
S" starting site used in training with partly closed off runway
▬ hurdle
O goalbox with reward container
← recording of running time at this point

Figure 6.1. Square box containing two similar runways, one being white, the other black.

Rewards were presented in red plastic containers located against the backwall of the goal compartments. The liquid rewards were placed manually in the containers before the start of each trial. A standard reward consisted of .15 ml of water. When amount of reinforcer was shifted, volumes of either .30 ml or .05 ml were used. These amounts were chosen so as to resemble as much as possible the amounts of water consumed in the various periods of the previous free operant leverpress experiment (Chapter V). Other rewards used were .15 ml of an 8% sucrose solution (saccharose, weight/volume in tap water) and .15 ml of a .01% quinine solution (QHCL, weight/volume in tap water), when palatability of the reward was shifted. After each trial the alleys were cleansed with a damp sponge.

6.2.2. Procedure

The experiment was run by two experimenters, each one training and testing his own subjects. The experimental groups were divided equally between them: each experimenter trained subjects of all experimental conditions and as many subjects in the white alley as in the black one. All rats were placed on a 23-hr water deprivation schedule for three days prior to pretraining and given water during one hour per day. Thereafter, they were maintained on a 23 1/2 hr deprivation schedule. On pretraining and training days 30 minutes of free access to water was given after completion of the sessions.

Pretraining
Half the subjects were trained in the white alleyway, the other half in the

black one. On the first 5 days of pretraining subjects were allowed to explore the runway from point "S" (see figure 6.1) to the goalbox, the first part of the alley being closed off. The goal compartment was baited with .15 ml of water. After consumption of the reward and only if the subject turned back and left the last straight part of the runway, the container was refilled with .15 ml of water. The requirement of leaving that part of the alley was made to minimize the possibility of disturbing the animals by this manipulation. Exploration time lasted until subjects had consumed the rewards three times, or else maximally 5 minutes. If an animal failed to enter the goal compartment and drink even one reward within 5 minutes, it was placed in the goal compartment and given opportunity to drink. On days 6-7 subjects were placed in "S" and three trials were run. On days 8-10 the partition closing off the first part of the runway was removed and subjects were placed in the startbox, the startdoor being opened before. Upon leaving the start compartment the door was closed behind them. Number of trials was increased from 5 to 10 to 15 per day. All subjects that learned to drink from the watercup during pretraining completed the experiment.

Training

During acquisition 16 trials were given per day on 8 consecutive days. Typically, subjects were very slow during the first trial. Therefore, the first trial served as a warming-up and data from this trial were not used for analyses. At the start of a trial a rat was placed in the start compartment with the door closed. The timeclock was started at the opening of this door. The timer was stopped again as soon as the subject had crossed a line 30 cms from the backwall of the goal compartment with at least three of its legs. After it had consumed the reward or after maximally 3 minutes the subject was removed from the apparatus.
The rats were run in squads of 4 to 6 animals which resulted in an intertrial interval of 3-5 minutes, depending on the running times of the other subjects in the same squad. Squads were run in the same order each day and running order within a squad remained the same also.
During pretraining and training the goal compartment was baited with the amount of water used as the standard amount throughout the experiment. After completion of the 8 training days subjects were assigned to one of 5 groups; each group contained as many animals trained in the white alley as animals trained in the black alley; also, groups were composed in such a way that mean running times per group were equal. The groups thus formed were exposed to different rewards during the shift phase of the experiment (see below).The following groups were formed:
- group WW, the control group (n=7), receiving the standard reward of .15 ml during the nonshift as well as the shift trials;
- group WQ (n=7), receiving .15 ml of the .01% quinine solution during shifts;
- group WS (n=7), receiving .15 ml of the 8% sucrose solution during the shifts;
- group W.05 (n=6), receiving .05 ml of water during the shift trials;
- group W.30 (n=6), receiving .30 ml of water during shifts.

Following the 8 days of training, subjects assigned to the groups WQ and WS were given presentations of the quinine solution and sucrose solution in their home cages so as to reduce its novelty. This was done on three consecutive nontraining days.

Shifts

On 8 successive days all subjects were given 16 trials per day. The first trial being a warming-up trial as before, the next 6 trials were given as usually, with a .15 ml water reward. During trial 8, 9 and 10, subjects received changed rewards, as indicated in their group assignments. During these shift trials the apparatus was turned 180 degrees to prevent the animals utilizing extra-maze cues; thus, subjects originally trained in the black alleyway now ran in the white one, and subjects normally run in the white alleyway now were placed in the black one. The colour of the alleyway served to signal the changed reward conditions. After completion of the three shift trials, the apparatus was turned back again to its normal position and each subject received 6 additional standard trials in its usual runway. Thus, the three shift trials were preceded as well as followed by 2x3 standard trials.
N.B. During shift trials in which the quinine and sucrose solutions were administered, the liquid containers were exchanged also to prevent possible influences of taste residuals.

6.2.3. Results

Training
Running times or latencies to goalbox were converted to speed measures by reciprocal transformation (Traupman and Wong,1971; Bolles 1975b), yielding running speeds. The speed scores of each day were grouped in 5 blocks of three trials each and the median per block was taken as the block score (Figure 6.2a). Performance stabilized around a value of .111. After subjects were assigned to their respective groups, training data were considered per group. Table 6.1 shows mean speeds and standard errors of the means over the last 4 days of training. See also Figure 6.2a.

Table 6.1. Mean speed scores over the last 4 training sessions. Speed scores (1/running time) were averaged per group per day.

	WW n=7	WS n=7	WQ n=7	W.30 n=6	W.05 n=6
$\bar{X}$	.124	.106	.127	.107	.104
SE	.007	.006	.004	.012	.008

Multivariate trend analyses (Finn, 1977) were performed on the block scores of the last 4 days. Taking the data of all days together, none of the experimental groups deviated from group WW, as was to be expected on the basis of group assignments. Taken all groups together, no changes over days were found. Comparing experimental groups with control group WW revealed that most groups did not differ from group WW in trends. Only group W.30 demonstrated differing trends in the block scores of the second and third blocks (multiv. $F=4.0$; $df=3,26$; $p<.05$ and multiv. $F=5.06$; $df=3,26$; $p<.05$), since it did not change its running speed over the last 4 days, whereas control group WW did.

Shifts
Median speed scores per block of three trials were transformed into

difference-scores by subtracting a subject's block scores, averaged over the last 4 training sessions, from each of its corresponding block scores of the 8 shift sessions. These difference-scores were analyzed by means of multivariate trend analyses. Results show the following. Taken all days and all groups together, speeds did not change during the shift phase of the experiment as compared with those during training. Only during the third block of trials did subjects run significantly slower than before (multiv. F=40.98; df=1,28; p<.01), due to the shift conditions then in effect (Figure 6.2b).

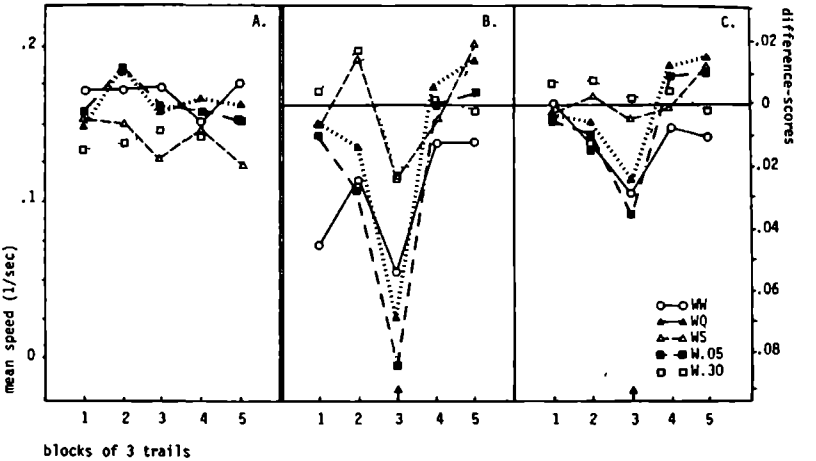


Figure 6.2.

a. Mean speed (1/running time) of the last 4 training sessions per block of 3 trials.
b. Difference-scores averaged over 8 shift sessions, given per block of 3 trials. Difference-scores were computed per block by subtracting each subject's mean scores of the last 4 training days from each of its corresponding shift session scores. The arrow indicates the block containing the shift in reinforcement (block 3).
c. Difference-scores averaged over the last 4 shift sessions, per block of 3 trials.

Trends were apparent on all blocks, due to mostly linear improvement of speed over days (in all cases, multiv. F>3.09; p<.05; see Figure 6.3). As said before, these improvements did not result in the overall scores to be significantly faster than during the training phase of the experiment. Differences between experimental groups and control group WW were absent, except for group W.30 being faster during block 3 (multiv. F= 6.97; df=1,28; p<.05).

To test for the possibility that differences between groups were emerging in the latter part of the experiment (see Figure 6.3), analyses were repeated for the last 4 days only (Figure 6.2c). This, however, did not change the total picture, except for the fact that most trend effects

disappeared (in blocks 2, 3 and 5).

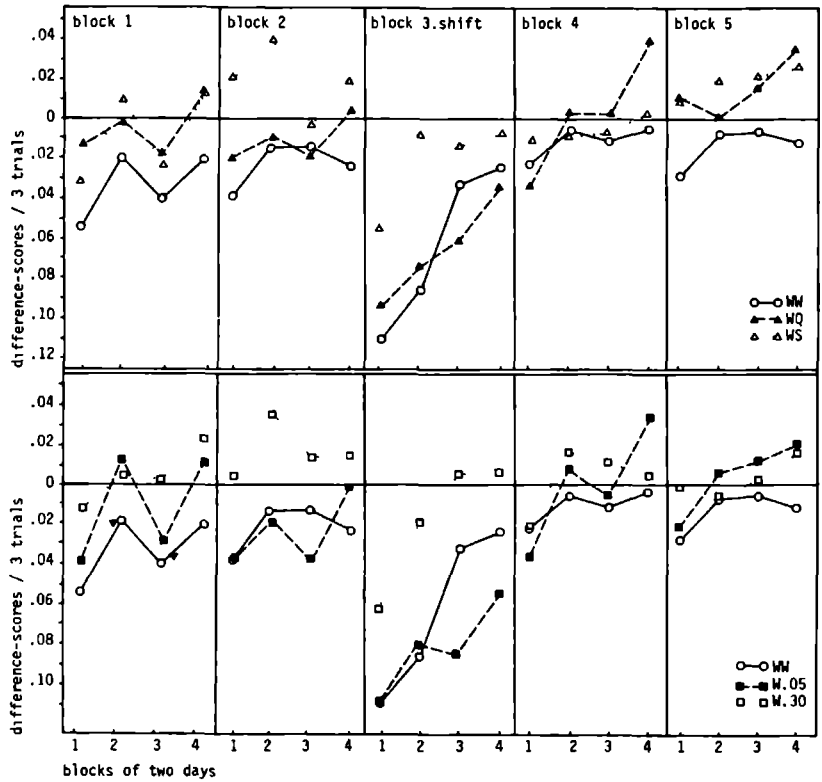


Figure 6.3. Difference-scores, presented per block of 3 trials, show changes over days. Difference-scores are computed by subtracting each subject's mean scores of the last 4 training sessions from each of its corresponding shift session scores. difference-scores have been averaged per two days. The upper series of graphs shows the control group with the two opposite palatability-of-reward groups; the lower graphs show the control group with the two amount-of-reward groups.

In summary: large decreases in running time were found in the trials of block 3: all subjects slowed down considerably, though group W.30 to a lesser degree than all other groups.
No postshift effects were found, neither contrast effects nor induction effects, neither positive nor negative. All groups performed essentially the same as the controls.

6.3. Experiment II. The effects of changes in solid rewards

It is often maintained that to obtain simultaneous contrast effects, at least the negative contrast effect, it is irrelevant whether liquid or solid rewards are used (Bolles, 1975a; Rashotte, 1979b). Nevertheless, in the previous experiment no indications were found for even the slightest contrast effects with variations in amount and quality of liquid rewards and with speed as the response measure. Since variations of solid rewards are most commonly employed to induce simultaneous contrast effects, the present experiment will investigate the effects of variations in amount and quality of solid rewards. The general procedure of the present experiment is exactly similar to the foregoing one.

6.3.1. Material

Subjects
Subjects were 55 naive male Wu rats (SPF63 Cpb; Loosli, 1975), obtained from TNO, Zeist. At the start of the experiment they weighed 210-250 grams. They were individually housed in Macrolon cages and kept in a stockroom under reversed day/night schedule. All training and testing took place in the dark period. Subjects had free access to water throughout the experiment; a few days before the start of the experiment they were gradually reduced to 90% of their free-feeding body weight. Thereafter, they were maintained at this level by being given a restricted amount of food per day. Each subject received its daily food ration following completion of training/test sessions. From the original 55 rats six were used for a preliminary study concerning taste preferences and 39 Ss completed the experiment. Ten others were discarded because they either did not consume the rewards offered or did not learn the running response.

Apparatus
The apparatus, fully described elsewhere (section 6.2.1, Figure 6.1) was a square wooden box, transformed into a white and a black "circular" runway. Food rewards, consisting of grinded Campden pellets, were placed manually in grey plastic containers, located in the goal compartments of the runways. The standard reward consisted of 75 mg pellet powder (compare with one Campden pellet weighing 50 mg). When amount of reward was varied, in the large-reward condition 150 mg was given, in the small-reward condition 25 mg.
Palatability of the reward was changed by adding either 1.2% quinine (QHCL, weight/weight of powdered pellets) or 32% sucrose (Saccharose, weight/weight of powdered pellets) to the reward powder. Both concentrations were chosen on the basis of preference tests of six rats in a preliminary study. See below.

6.3.2. Procedure

Determination of concentration of flavouring
To decide which percentage of quinine and sucrose respectively had to be added to the food powder, six rats were offered 15-minutes choices in their home cages. One of two food trays always contained 20 g plain pellet powder, the other tray contained a varying amount of quinine or sucrose added to the 20 g powder. After 7 1/2 minutes tray locations were reversed

to counteract possible location preferences. Before and after choice tests, food containers plus contents were weighed and the differences were taken to represent the amount eaten from each container. Two sucrose concentrations and nine quinine concentrations were tried before satisfactory results were obtained. One choice test was given per day.

Training and shifts

The experiment was run by two experimenters, each training and testing his own subjects. All groups were divided equally between them. Thus, each trained subjects of all experimental groups and as many subjects in the white alley as in the black one.

The procedure followed was identical to that employed in the previous experiment (section 6.2.2); after 10 days of shaping and pretraining, training was begun and continued for 8 days, followed by 8 days utilizing the shift procedure. 16 trials were given per day, the first trial serving warming-up purposes, and shifts in the reward being presented during the trials 8, 9 and 10. Subjects had access to water between trials.

Groups were formed on the basis of speed scores of the last 4 training days:

- group FF (n=8), the control group, receiving the standard amount of 75 mg of food powder during shift trials;
- group FQ (n=8), receiving 75 mg of food powder adulterated with 1.2% quinine during shifts;
- group FS (n=8), receiving 75 mg of the reward containing 32% sucrose during shifts;
- group F150 (n=8), receiving 150 mg of food powder during shifts;
- group F25 (n=7), receiving 25 mg of food powder during shifts.

Shift trials were signalled in that rats trained in the white alley were run in the black alley and vice versa.

N.B. Groups FQ and FS had been exposed to quinine and sucrose adulterated food presentations respectively before entering the shift phase of the experiment.

Table 6.2. Amount of pellet powder consumed during 15-min presentations.

SUCROSE concentration	SUCROSE grams	STANDARD pellet powder grams	QUININE concentration	QUININE grams
16	2.8	2.8	0.1	3.2
32	4.9		0.3	2.5
			0.4	1.3
			0.75	1.1
			1.0	1.0
			1.2	0.7

6.3.3. Results

Flavour concentrations chosen

The often used sucrose concentrations of 16% and 32% were offered in a two-choice situation, the alternative being plain pellet powder. Results

of amounts consumed indicated that the 32% sucrose powder was substantially preferred over the plain pellet powder (see Table 6.2). This concentration therefore was used in the experiment.
The finding of a suitable quinine percentage proved much more complicated. Seven concentrations of increasing intensity had to be tested before a satisfying relative consumption was reached (see Table 6.2). The concentration of 1.2% seemed to be disliked sufficiently to serve as a reward in the shift phase of the experiment.

Training
Performance was expressed in running speeds (1/running time). The speed scores of each day were then grouped in 5 blocks of three trials per day and the median per block was taken as the block score. Running speeds stabilized at an average .206, which is much faster than in the previous experiment. Most subjects tended to run somewhat faster in the latter trials than in the first trials of each day (see figure 6.4a).

After subjects were assigned to their respective groups, training scores were considered per group and group averages and standard errors were computed. The results are shown in Table 6.3.

Table 6.3. Mean speed scores (1/running time) over the last 4 training sessions. Speed scores were averaged per group per day.

	FF n=8	FS n=8	FQ n=8	F150 n=8	F25 n=7
$\bar{X}$	.197	.234	.188	.206	.206
SE	.005	.011	.003	.007	.009

Multivariate trend analyses (Finn, 1977) were performed on the block scores of the last 4 training days, in which each experimental group was compared with control group FF. No differences were found between groups, nor were trend effects or trend differences revealed.

Shifts
Median speed scores per block of three trials were transformed into difference-scores: each subject's training block scores, averaged over the last 4 days, were subtracted from its corresponding daily block scores of the shift phase of the experiment. On these difference-scores multivariate trend analyses were performed.
Overall, all experimental and control subjects ran slower during this phase than during training in block 3, presumably due to the shifted conditions (Multiv. $F=10.49$; $df=1,34$; $p<.01$) and also in block 4 (Multiv. $F=19.44$; $df=1,34$; $p<.01$). See Figure 6.4b.
In block 3 all groups showed a rapid linear recovery of speed over days (Multiv. $F=19.44$; $df=7,28$; $p<.01$) (Figure 6.5). The same was found in block 4 (Multiv. $F=2.80$; $df=7,28$; $p<.05$). Experimental groups never differed from group FF, except group F150, which ran slower than the controls in block 2 (Multiv. $F=9.18$; $df=1,34$; $p<.01$).

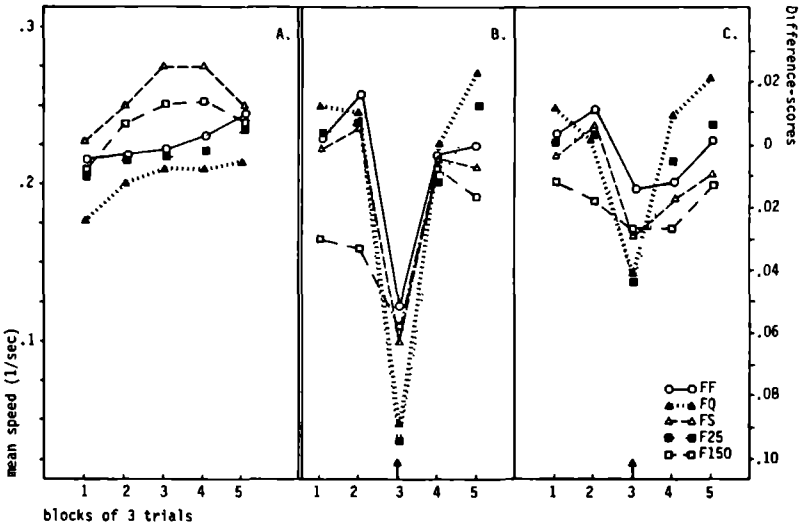


Figure 6.4.

a. Mean speed (1/running time) of the last 4 training sessions, per block of 3 trials.

b. Difference-scores averaged over 8 shift sessions, given per block of 3 trials. Difference-scores were computed by subtracting each subject's mean scores of the last 4 training sessions from each of its corresponding shift session scores. The arrow indicates the block containing the shift in reinforcement (block 3).

c. Difference-scores averaged over the last 4 days of testing, per block of 3 trials.

Figure 6.5 suggests that differences might have developed in the latter phase of the experiment, particularly in the blocks 4 and 5. Trend analyses performed over the last 4 days confirmed this impression for group FQ: during block 4 and block 5 group FQ ran significantly faster than control group FF (Multiv. $F=5.10$; $df=1,34$; $p<.05$ and Multiv. $F=5.58$; $df=1,34$; $p<.05$ respectively), thus showing a positive contrast effect. No trend differences were found (Figure 6.4c).
From Figure 6.5 it can be seen that, particularly in the latter days, the experimental groups are diverging during block 3: group FQ becomes slower than group FS and group F25 becomes slower than group F150. In contrast, during the blocks 4 and 5 the reverse seems to be the case.

In summary: large shift effects were found in block 3, all subjects slowing down, irrespective of direction of reward shift. This drop in responding, however,rapidly decreased and in the latter days of testing the experimental groups were diverging in accordance with direction of shifts. No contrast effects were found, except for the latter days positive contrast effect of group FQ, due to it showing sharp increases in speed in block 4 and block 5.

It is somewhat puzzling that individual data do not show clear indications for this positive contrast effect in group FQ, whereas they tend to do in group F150.

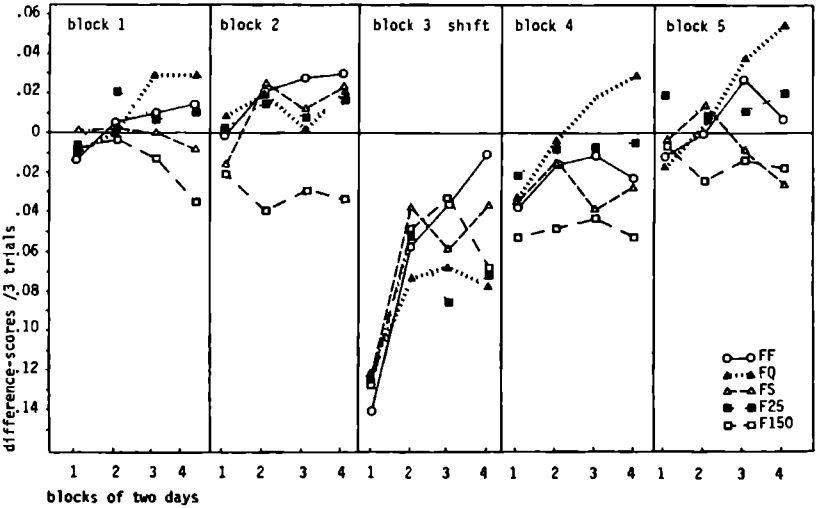


Figure 6.5. Difference-scores, presented per block of 3 trials, show changes over days. Difference-scores are computed by subtracting each subject's mean scores of the last 4 training sessions from each of its corresponding shift session scores. Difference-scores have been averaged per two days.

6.4. General discussion

The first result that needs to be considered is the finding that changing the colour of the alleys had such a markedly disrupting effect on performance. Whatever group they belonged to, and whether water reinforced or food reinforced, all subjects invariably slowed down considerably. In the majority of discrete trial contrast studies, rats have been trained in black and white alleys, one alley colour signalling one reward value, and the other alley colour another. However, usually no pretraining phase comparable to ours, is employed: the two alleys are run in from the first day of training onwards; that is, the contrast effects develop while the running task and the discrimination is mastered. Even though we introduced the signal (alley colour) abruptly in the course of the experiment and did so deliberately to increase comparability between the present runway test and the prior free operant tasks (Chapter IV and V), performance disruption was not expected to be so large, because the sudden introduction of a signal in the free operant situation caused no drop in response rates. This undoubtedly neophobic reaction (E.D.Capaldi, 1978; Braveman, 1978) disrupted performance only temporarily: all groups rapidly recovered to levels in accordance with their respective reward values. It is probably mainly because testing has not been carried on long enough that return to

baselevel by the control groups was not yet accomplished and that experimental groups did not yet differ from the controls during the shift trials.

It is clear that, notwithstanding the severe response decrement preceding it, no contrast effects were found, whether rewards were liquid or solid, and whether amount was shifted or quality. The only contrast effect emerging in the latter days of testing was a positive contrast effect after the presentation of quinine adulterated food rewards.
This finding of a positive contrast effect in group FQ in the solid food situation is rather unusual in many respects.
First of all, the simultaneous positive contrast effect is generally not easy to detect (e.g. Black, 1968; Mackintosh, 1974b; Flaherty, 1982).
Secondly, the use of speed as a response measure poses limits for the occurrence of positive contrast effects. If the occurrence of ceiling effects is considered a viable explanation of the general absence of a positive contrast effect, it is very puzzling that a positive contrast effect did occur in the solid reward situation and not in the liquid reward experiment, since subjects were running faster in the former study.
Finally, a simultaneous positive contrast effect following shifts in quality of the reward has been reported mainly with liquid rewards and lick rate as the response measure (Flaherty and Avdzej, 1974, 1976; Flaherty et al., 1977); we, however, were unable to demonstrate a positive contrast after quinine presentations in the liquid rewards experiment with a locomotor response, whereas we did in the solid rewards experiment.
Varying amount of reward has been largely unsuccesful in producing positive contrast effects (Bower, 1961; McHose and Ludvigson, 1965; Ludvigson and Gay, 1966; Mackinnon,1967; Peckham and Amsel, 1967; Gavelek and McHose, 1970; Shanab and McCuiston, 1970; Chechile and Fowler, 1973). Though we were unable to do so too, individual data of the groups that had their rewards reduced during shift trials (Experiment I, group W.05; Experiment II, group F25) revealed at least a tendency towards positive contrast effects (one-tailed t-tests, see below).

The absence of a negative contrast effect in both experiments is hard to explain, particularly so because it is such a commonly found phenomenon under a wide variety of conditions. Speed measures do in fact offer ample opportunity for negative contrast effects to develop. Nevertheless, no negative contrast effects were found, neither in the solid reward experiment nor in the liquid reward test.
It is well known that within limits instrumental performance increases consistently with improved quality/amount of reward and vice versa (Goodrich, 1960; Kintsch, 1962; Snyder, 1962; Rosen, 1966; Gonzalez and Bitterman, 1969; Ison and Glass, 1969; Wike and Chen, 1971; Daly, 1972; Barnes and Tombaugh, 1973; Bolles, 1975a). Despite this, negative contrast effects are reported more often than not after shifts in amount of reward, but much less so after varying the quality of reward. Ison and Glass (1969), for example, demonstrated the occurrence of a negative contrast effect following size reductions of the reward, but were not able to demonstrate the effect after quality reductions. However, others did find the latter effect (Rossman and Homzie, 1967; Flaherty et al., 1973a; Flaherty and Avdzej, 1974, 1976; Flaherty et al., 1977).
Our failure to produce a negative contrast effect by varying amount of reward, whether solid or liquid, is most strikingly at odds with the majority of studies designed to produce it (e.g. Bower, 1961, 1962;

Ludvigson and Gay, 1966; Matsumoto, 1969; Gavelek and McHose, 1970; Chechile and Fowler, 1973).
It might be argued that concentrations and amounts/volumes chosen were not dissimilar enough. Size of contrast effects is said to be directly related to the degree of disparity between the reward values used (Ludvigson and Gay, 1966; Spear and Spitzner, 1966; Flaherty, 1982).
- The quinine and sucrose solutions used in the liquid rewards experiment have been tried before in a free operant leverpress situation and proven sufficient to produce very different response rates, for that situation at least. It is not clear why they wouldn't suffice in a runway test. However, Ison and Glass in their study cited above (1969) reported that functional differences between two reward qualities used in a vain attempt to produce a negative contrast effect, were actually greater than between two reward sizes used that did produce the effect. Thus, the size of the reward disparity judged from diverging response rates is no guarantee for its power to induce contrast effects.
- The situation for the quinine and sucrose concentrations in the solid food reward experiment is even less clear. The concentrations consumed in a choice test did suggest that they would suffice. However, consummatory responses and instrumental responses for the same reward value are not necessarily related (Kraeling, 1961; Robbins, 1969; Bolles, 1975a; Beck, 1978). The quinine concentration did in fact induce a positive contrast effect.
Our data suggest that at least the quinine concentrations used sufficed, since in the solid reward runway situation as well as in the free operant leverpress situation (Chapter IV and V) it produced positive contrast effects. The sucrose concentrations, though inducing higher response levels in the free operant task, did not produce negative contrast effects in both the runway and the leverpress tests.
- It is more difficult to judge whether the volumes/sizes used in the present experiments were suitable. The diverging performance levels of groups W.05 and W.30 during block 3 in the liquid reward experiment are an indication that at least these volumes were capable of producing different response levels. That this need not be sufficient was shown in the Ison and Glass (1969) study cited above.
- The different amounts used in the solid reward experiment, however, not even produced performance differences. So, they may not have been different enough.
Another group of data bears perhaps some importance to the absence of almost any contrast effect in our tests. It has been reported that introduction of a novel stimulus coincidentally with the shifted reward reduces contrast effects (E.D.Capaldi, 1978; Lombardi and Flaherty, 1978). Since subjects ran in another, unfamiliar, runway during the shift trials, the amount of novelty brought about by the changed colour and undoubtedly also changed odours probably has been too much. If small tendencies towards contrast effects occurred, they might have been masked by a reduction in this tendency due to the novelty of the runway used in the shift trials.
Since in previous experiments negative contrast conditions have resulted in rather dishomogeneous response patterns within the groups concerned, individual data were tested by means of one-tailed t-tests, comparing each subject's 8 shift sessions with its last 4 training sessions. In the experiment using water as the reward, none of the groups showed any uniformity in responding, except group W.05, whose individuals tended towards a positive contrast effect. In the experiment employing food

rewards, groups FF, FQ and FS also showed dishomogeneous response patterns. However, the subjects of group F25 tended towards a positive contrast effect.

The latter findings are remarkable, as they are not reflected in the group results, where group FQ demonstrated a positive contrast effect and group W.05 in Experiment I and group F25 in Experiment II did not.

Thus, the results do also indicate that between-Ss and within-Ss comparisons are not only differently sensitive to the various experimental manipulations (McHose, 1963; Hamm, 1967; McHose and Gavelek, 1969; Mackintosh, 1974b; Rashotte, 1979b), but that they do not necessarily produce similar results either (compare the group data and individual data of the groups W.05 in Experiment I and FQ and F25 in Experiment II; see above).

Finally, it is entirely clear that the too short period of testing may largely be held responsible for the absence of contrast effects, as the only effect we found, did emerge in the latter days of testing. Discrete trial contrast effects have often been found to develop slowly (Rashotte, 1979b).

CHAPTER VII.

THE INFLUENCE OF LESIONS IN THE PREFRONTAL CORTEX ON CONSUMMATORY AND INSTRUMENTAL BEHAVIOUR FOR WATER, SUCROSE SOLUTIONS AND QUININE SOLUTIONS

in collaboration with dr.C. Sennef

7.1. Introduction

The present study attempts to combine a behavioural technique, the contrast paradigm, used to study appetitive/aversive interactions with the analysis of dysfunctions in the appetitive/aversive mechanisms induced by lesions in the prefrontal cortex (PFC).
Indications are many that the prefrontal cortex, which is considered a cortical continuation of the limbic system, is involved in the regulation of particularly appetitive behaviour (Sennef, 1985). This cortical area may be subdivided into several regions, two of which are involved in the present study: the medial PFC and the sulcal PFC.
In order to clarify the role of the PFC, it is necessary to differentiate behaviour into instrumental behaviour and consummatory behaviour. Instrumental behaviour is the behaviour aimed at reaching some not directly available stimulus, whereas consummatory behaviour is the final behaviour towards that stimulus once it is reached (e.g. eating). The findings concerning involvement of the prefrontal cortex may be summarized as follows.

1. Bilateral damage to the sulcal prefrontal cortex causes considerable impairments of consummatory behaviour; this is found in normal eating and drinking behaviour (Kolb, 1974b; Kolb and Nonneman, 1975; Sennef, 1985) as well as in the eating behaviour induced by stimulation of the lateral hypothalamus (Sennef, 1985). Medial PFC lesions affect both kinds of behaviour only slightly.
2. In contrast, strong evidence exists that the medial PFC is involved in instrumental behaviour, whereas the role of the sulcal PFC in this behaviour is less clear. Following bilateral medial prefrontal lesions a temporary reduction of instrumental behaviour directed towards obtaining rewarding electrical stimulation in the lateral hypothalamus was found; sulcal lesions had no such effects (Sennef, 1985). It has also been demonstrated that medial prefrontal damage caused a decrease in running speed in a runway (Glass et al., 1969; Gurowitz et al., 1970), as well as declining response rates on a CRF schedule in a Skinnerbox (Numan and Grant, 1980). However, Kolb et al. (1974) did not find effects of medial PFC lesions on responding on a CRF schedule when they tested subjects several months after surgery, whereas sulcal lesions did cause a depressed response rate at that time. Their medial lesions, however, included only the anterior cingulate area and left the prelimbic area unaffected. Besides, the long recovery time after which was tested seems an important determinant of their results. The effects of medial PFC lesions have been described as a reduction in approach tendencies, c.q. instrumental behaviour (Glass et al., 1969; Gurowitz et al., 1970).

In short: the sulcal PFC seems to be involved in consummatory behaviour, whereas the medial PFC probably plays a role in instrumental behaviour.
In the present experiments the influence of lesions in either the medial or

the sulcal prefrontal cortex on consummatory as well as on instrumental behaviour directed towards appetitive stimuli will be investigated.
Quality and intensity of consummatory as well as instrumental behaviour in a learning task are determined mainly by the prevailing physiological state of the subject on the one hand, and by the particular properties, the incentive value, of the stimuli to be obtained on the other hand (Bolles, 1975a; Bindra, 1976; see also Chapter II). Thus, deficits in the sensory and motor abilities of the organism aside, changes in behaviour may be induced by changes in physiological state (e.g. deprivation level), and/or changes in incentive value of the stimulus (quantity, quality, taste etcetera).
To gain a better insight in the influence of PFC lesions on behaviour with respect to appetitive stimuli, the incentive value of an appetitive stimulus was varied; deprivation level was held constant. This was done by exposing the subjects to water rewards as well as either a more preferred sucrose solution or a less preferred quinine solution.
In the first experiment to be described the influence of PFC lesions on the consumption of plain water, quinine solutions or sucrose solutions is investigated. As for the role of taste in consummatory behaviour, Kolb et al. (1974) found that medial PFC lesions resulted in finickiness: addition of quinine to solid food caused a stronger reduction of food intake in medially lesioned subjects than in subjects with sulcal or sham lesions.
In the second experiment instrumental behaviour, operant responding on a VI schedule, was examined. The influence of incentive value (taste) of the reward was investigated in the contrast paradigm employed before (see Chapter V). Attention is focused on the influences of prefrontal lesions, first, on behaviour changes directly induced by changes in reward quality during shifts, and, secondly, on the contrast effects following the shifts. In a series of experiments reported before (Chapter IV and V), normal unoperated rats demonstrated positive contrast effects upon returning to regular reward conditions following negative shifts (quinine) of reinforcement. Rats exposed to a positive shift (sucrose) in the reward value did not show the expected negative contrast effects. On the contrary, their response level remained higher than before (positive induction effect).
Examination of the effects obtained after PFC lesions might offer some insight into the role of the prefrontal cortex in the effectuation of appetitive behaviour. The entire pattern of instrumental behaviour within sessions will be carefully analyzed.

7.2. Experiment I. The influence of prefrontal cortex lesions on the consumption of water, sucrose and quinine solutions

7.2.1. Methods

Subjects
The experiment employed 27 male Wu rats (SPF63 Cpb) that had served before in an experiment measuring light-aversion and activity in the open field (Sennef, 1985). The control group (n=10) had been sham-operated, the others had received bilateral lesions in either the medial (n=10) or the sulcal (n=10) PFC. Details of the surgical procedures and anatomical results have been reported elsewhere (Sennef, 1985). Grosso modo, lesions were identical with those of the subjects that will be described in

Experiment II. In the present experiment, nine subjects of each of the above-mentioned groups were tested. Time between operation and the present experiment was six weeks. Subjects were housed individually under reversed day/night schedule and received food ad lib. At the start of the experiment subjects averaged 368 g of weight; the three experimental groups did not differ in this respect.

Procedure

Prior to testing, all rats were placed on a 23-hr water deprivation schedule; they were allowed to drink water every day from 11.00-12.00 a.m. in the home cage. After 4 days of adaptation to this schedule, water consumption was measured during the first ten minutes of each one-hour water presentation. During the remaining 50 minutes water was given as usually. Then, following 3 days of the same deprivation regime a .01% quinine solution (QHCL, weight/volume in tap water) was offered during the first 10 minutes of the one-hour presentation in the homecage and amount taken was measured. This was repeated on 4 successive days. Another 3 days later, the same procedure was repeated with an 8% sucrose solution (saccharose, weight/volume in tap water) on 4 successive days. Weights of subjects were recorded at the start and after completion of the experiment.

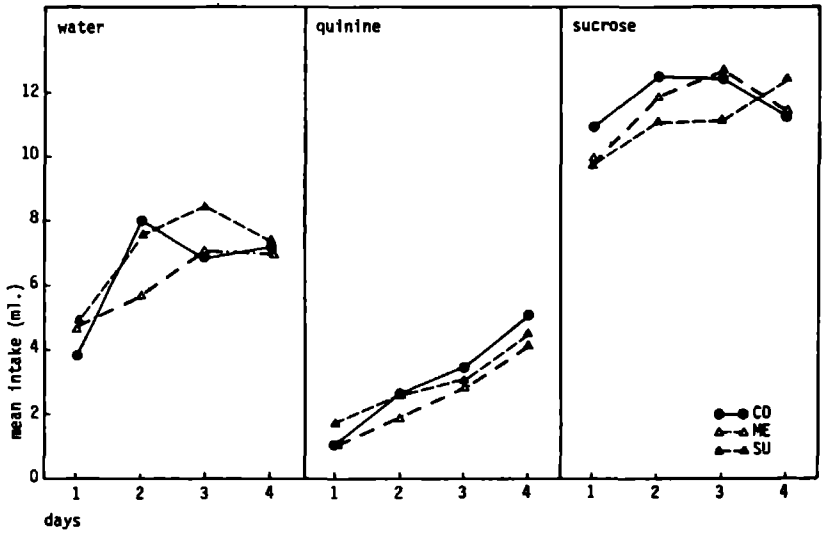


Figure 7.1. Consumption of water, quinine and sucrose during 10-min presentations following 23 hr deprivation; results are given for the sham control group (CO), the group with medial (ME) and sulcal (SU) PFC lesions.

7.2.2. Results

Figure 7.1 shows the mean consumption of each of the three liquids offered

per 10-min test. Average amounts consumed are 6.7, 3.7 and 11.4 ml per 10 minutes for water, quinine solution and sucrose solution respectively. A 3(groups) x 3(taste of liquid) x 4(days) repeated- measures Analysis of Variance (Winer, 1971) showed that the effect of taste was highly significant ($F=195.4$; $df=2,48$; $p<.01$); subjects consumed more of the sucrose solution and less of the quinine solution if compared with the water consumption. The factor days was significant also ($F=27.3$; $df=3,72$; $p<.01$) and reflects the increase in consumption of all three liquids over days. This increase, however, was different per liquid, as is revealed by a liquid x days interaction ($F=3.66$; $df=6,144$; $p<.01$); quinine consumption increased more markedly than consumption of the other liquids. Neither type of prefrontal cortex lesion had any effect on the consumption pattern of these liquids ($F=0.34$; $df=2,24$).

7.2.3. Discussion

A clear influence of taste stimuli on the water consumption was demonstrated. The results of this experiment closely resemble those of previous studies (Chapter IV and V). A strong neophobic reaction seems responsible for the depressed consumption on the first day of testing, probably attributable to the novelty of the testing procedure, as it is apparent in the water data also; presumably, after two days adaptation has taken place and water consumption then stabilizes around 7.4 ml. Introduction of new flavours causes consumption to decrease temporarily below the level actually reflecting the subjects' like and dislike of the solutions offered. This again might represent a neophobic reaction, this time induced by the novel flavours.
Neither medial nor sulcal prefrontal lesions - after a long period of recovery at least - seem to have any effect on amounts of liquids consumed, nor on the pattern of consumption over days. These findings are at odds with reports about increased finickiness for quinine flavours after medial prefrontal lesions (Kolb and Nonneman, 1975). However, these results were obtained with quinine added to solid food and consequently with much higher quinine concentrations than the concentration chosen here which was offered in water.

7.3. Experiment II. The influence of prefrontal cortex lesions on operant responding under water deprivation and on response changes induced by shifts in the quality of reward

7.3.1. Material

Subjects
Subjects were 36 male Wu rats (SPF63 Cpb). At the start of the experiment they weighed 429 g (± 21). All housing conditions were the same as those described in the foregoing experiment.
Immediately prior to the present experiment the subjects had served for two months in the experiment described in Chapter V. In that study the influence of changes in quality and quantity of the reward on operant responding on a VI schedule was investigated. Thus, all subjects have been kept on a 22 1/2 hr water deprivation schedule for a long time; they have been given shaping and CRF training sessions and have had considerable experience on a VI-30 sec schedule (25 sessions); and finally, they have

experienced reward shifts before in a paradigm similar to the one employed in the present experiment: almost all subjects have been exposed to reward changes, either in quantity or in quality.

Apparatus
The set of 8 experimental chambers (Campden, Model 410) has been fully described elsewhere (see Chapter V). The one difference concerns the cue used for signalling the changed reinforcement conditions. In the present experiment a 1.000 Hz tone, 2 dB above background noise, and on during the full period of change, was used instead of the former light cue, so as to minimalize a possible carry-over effect of learned expectations from the former experiment. The tone was delivered through a speaker mounted in the ceiling of the test box.

7.3.2. Surgical methods and histology 1)

Surgery
All operations were carried out under Nembutal anesthesia (20 mg/ml; .225 ml/100 g; i.p.). Lesions were produced by a Radionics Radiofrequency Lesion Generator (RFG-4), with the anode inserted stereotactically in the brain and an anal cathode. The stainless steel electrode had a length of 100 mm and was insulated with exception of the tip (1.5 x 0.7 mm). For the medial lesions (group ME) current strength was maintained during 60 seconds at the level that produced a tip temperature of 52-53 degrees Celsius; for the sulcal lesions (group SU) a tip temperature of 58 degrees was aimed at and maintained for the same period. Two medial prefrontal cortex lesions were made, one above the other, via the vertically inserted electrode; coordinates were 10.6 mm anterior,0.8 mm lateral, and 5.0 and 2.6 mm respectively below skull surface (Pellegrino and Cushman, 1967). A single sulcal lesion was placed bilaterally with the coordinates: 10.6 mm anterior, 3.9 mm lateral and 5.4 mm below skull surface; the electrode was inserted under a 16 degrees angle from the median plane. Sham operations (control group CO) contained incision of the skin and the bilateral drilling of holes in the skull surface: for half of the subjects these holes were drilled above the medial PFC, for the others this was done at the same place as for the sulcally lesioned group. Thus, surgical treatment was identical to that of the lesioned groups, except that no electrode was inserted. The lesions were bilateral in all cases.
After surgery rats were returned to their home cages and received food and water ad lib for 4 days. Additionally, lesioned subjects received mashed food during the first 3 recovery days. Following 7 days of recovery, training was resumed.

Histology
After completion of the experiment subjects were sacrificed by Nembutal overdose (60 mg/ml; .25 ml/100 g; i.p.), and perfused through the heart with a .9% saline solution, followed by 4% Formalin. The brains were removed, soaked in 4% Formalin for three weeks and embedded in Albumin jelly. They were frozen and sliced in 50 µm sections. Every fourth section from the frontal area was stained with cresylviolet. Lesions were then mapped onto maximally 5 standard diagrams (anterior 11.6, 11.0, 10.4,

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1) Lesions and anatomical data collection were performed by dr.C.Sennef

9.8 and 9.2 mm) from the Pellegrino and Cushman Stereotactic Atlas (1967). By means of a surface analysis device (Kontrom Messgeraete, type Digiplan) extent of damage was determined for each level; thereupon total amount of damage was estimated by means of methods described by Sennef (1985).

7.3.3. Test procedure 2)

All subjects were kept on a 22 1/2 hr water deprivation schedule, except for a few days immediately after surgery. They were given access to water during one hour after each test session.
During Phase I (presurgery phase) of the present experiment subjects were submitted to 10 daily sessions of retraining on a randomized VI-30 sec schedule for water reward. Each session lasted 24 minutes and consisted of 5 periods of 4 minutes each in which the schedule was in effect, separated by 1-min time-out periods. In the time-out periods all lights in the box were switched off and the lever was retracted. A standard reinforcer consisted of .05 ml water. As all subjects were rather experienced VI-30 sec performers (see section 7.3.1), this phase rather than learning served the unlearning of associations formed before.
At this stage, subjects were grouped into two groups (n=18 each) on the basis of their prior experiences (Chapter V): a QUININE group which later on in the experiment received quinine rewards, was composed of subjects that have experienced negative shifts in reward before; and a SUCROSE group, composed of subjects that either had experienced positive reward shifts or had served as controls.
Thereupon, the two groups thus formed were each subdivided into three subgroups (n=6 each) on the basis of their mean response frequencies over the last 5 presurgery sessions: control subjects that were to receive sham operation (CO), medial prefrontal cortex lesions (ME) or sulcal prefrontal cortex lesions (SU). Thus, six groups were formed. Subsequently, surgery was performed (see section 7.3.2).
After surgery subjects received food and water ad lib for 4 days; subjects with PFC lesions were given mashed food during the first 3 recovery days. Weights were taken every day.
After 7 days of recovery, during Phase II, subjects were retested on 5 successive days under the same conditions as before surgery (Phase I).
Then, the shift phase, Phase III, of the experiment started. Subjects were tested on 10 successive days on the same VI-30 sec schedule as before. However, in the third period a reward consisting of a .01% quinine solution (QHCL, weight/volume in tap water) instead of water was given to the quinine groups; the sucrose groups received a 8% sucrose solution (saccharose, weight/volume in tap water) instead of the water reward during the third period. In the other periods the regular water reward was given. This change in the quality of the reward during the third period was cued by a tone signal of 1,000 Hz.
For each subject response rates per minute were registered during the entire experiment.

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2) Behavioural data were collected by J.P.M. Receveur

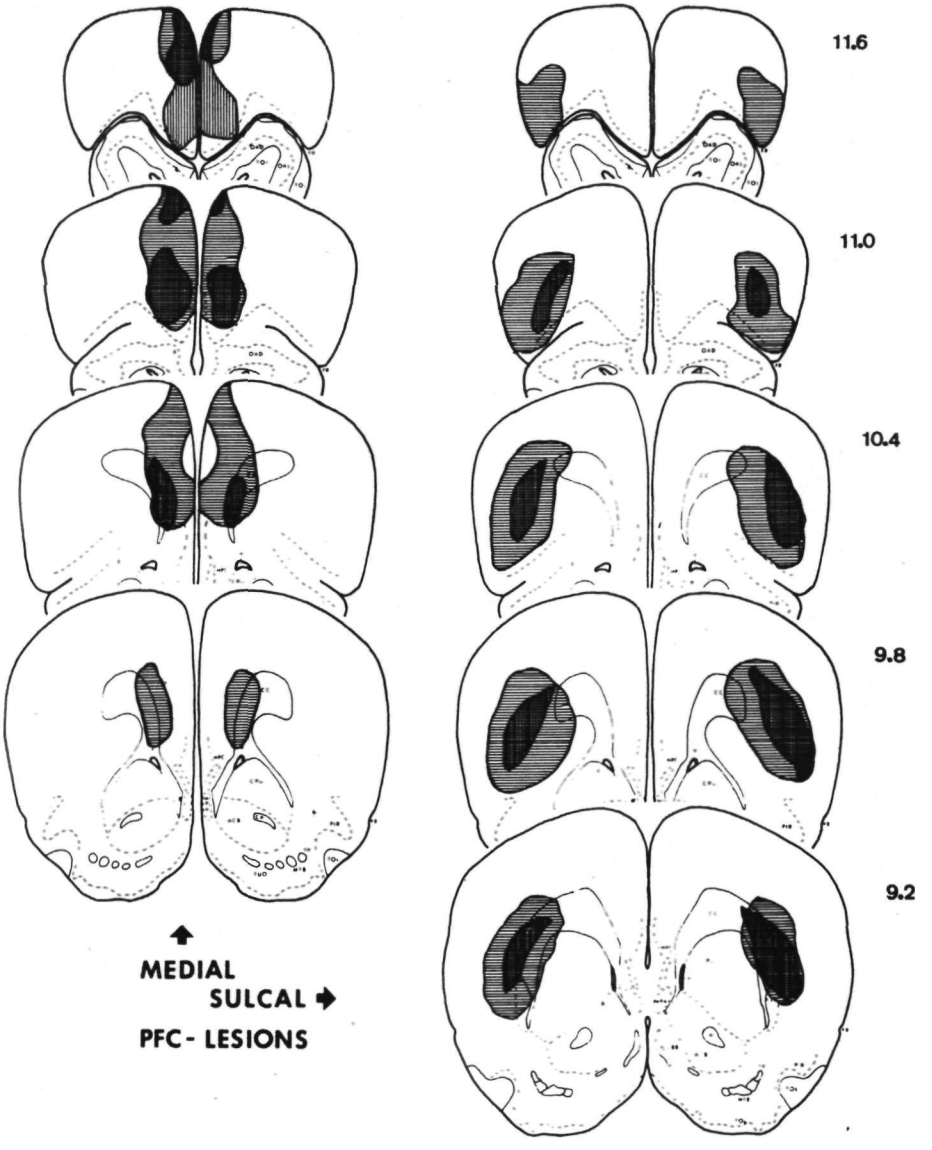

Figure 7.2. Diagrammatic representations of the largest (=) and smallest (¦¦) lesions of the medial (left) and sulcal (right) PFC. Diagrams are from Pellegrino and Cushman (1967). The levels presented are 11.6, 11.0, 10.4, 9.8 and 9.2 mm anterior.

7.3.4. Anatomical results

Diagramatic representations of the largest and the smallest medial and sulcal lesions on five frontal levels are shown in Figure 7.2. The medial PFC lesions typically destroyed the most rostral part of this region; the main areas damaged are the prelimbic region and the rostral part of the anterior cingulate area (i.e. the ventromedial PFC). Slight damage was usually also sustained by the Genu of the corpus callosum. Estimated size of the lesion was 8.1 $\pm$ 2.0 mm3; the deviation was mainly located in its rostral extent.
Ventrolateral PFC lesions were located somewhat more caudally than the medial PFC-lesions. Rostrally, mostly superficial layers of the lateral orbital area and the anterior insular area were destroyed; caudally, deeper layers of the anterior insular area were also affected. In all subjects, the lateral part of the Genu, the deeper layers of the lateral neocortex, just above the anterior insular area, and occasionally the rostral part of the claustrum sustained damage also. Estimated size of the sulcal lesions was 11.1 $\pm$ 3.9 mm3, which is slightly larger than the medial PFC lesions. Lesions varied mainly in their rostral extent as well as caudally in amount of tissue damaged. Involvement of the Genu of the corpus callosum in both lesions means at least partial damage to efferent and afferent fibers from and to both prefrontal areas.

7.3.5. Behavioural results

Response rates per period of 4 minutes served as the basic data on which statistical analyses were performed. For all phases after surgery, analyses were aimed at revealing whether differences in response patterns did exist between sham operated and lesioned groups, in comparison with presurgery performance. To this end, difference-scores between pre- and post-surgery scores were computed for each period per subject. Because during each phase of the experiment tests were repeated several times, this was done by means of a multivariate analysis for repeated measurements (Finn, 1977), in which each lesion group was compared with the sham control group. First, overall group means were tested, and, secondly, changes over days (trend analyses).

Phase I. Presurgery retraining
Prior to surgery all subjects were given 10 daily training sessions on a VI-30 sec schedule with .05 ml water as a reward. Only the results of the last 5 days have been analyzed in order to determine whether pooling of the data over days would be allowed, the pooling serving the goal of providing a reliable baseline against which to test lesion effects.
After completion of this phase, the three groups (CO, ME and SU) were formed on the basis of response frequencies of the last 5 training sessions in this phase. Thus, differences between groups were not to be expected. Trend analyses performed on the data of the last 5 days, for each period separately, confirmed this: no differences between groups were found; at this point in the experiment groups can be considered identical. Response rates during the last 5 presurgery training sessions averaged 454 responses per session.
No changes occurred over days, neither per period nor in the total response scores per day. Thus, response rates might be considered stabilized and the means of the response frequencies of the last 5 days prior to surgery

can safely be taken as a point-of-reference for postsurgery performance. Response rates within session declined from approximately 125 responses in the first period of 4 minutes to some 35 responses in the last 4 minutes of responding. Response rate in the latter period was, however, almost always high enough to obtain all available rewards. Thus the pattern of responding gained efficiency.

Phase II. Postsurgery training

The influence of the lesions on responding on a VI-30 schedule was determined by comparing changes in performance per period with the individual mean scores per period of the presurgery sessions. Thus, response rates per period were transformed into difference-scores, by subtracting a subject's mean of the last 5 presurgery sessions from each of its present sessions. Figure 7.3 shows the mean difference-scores per period for the three experimental groups CO, ME and SU each. A multivariate trend analysis has been performed on these transformed data, comparing ME with CO and SU with CO. All groups taken together, response rates in Phase II were similar to those in Phase I. There were, however, some group differences.

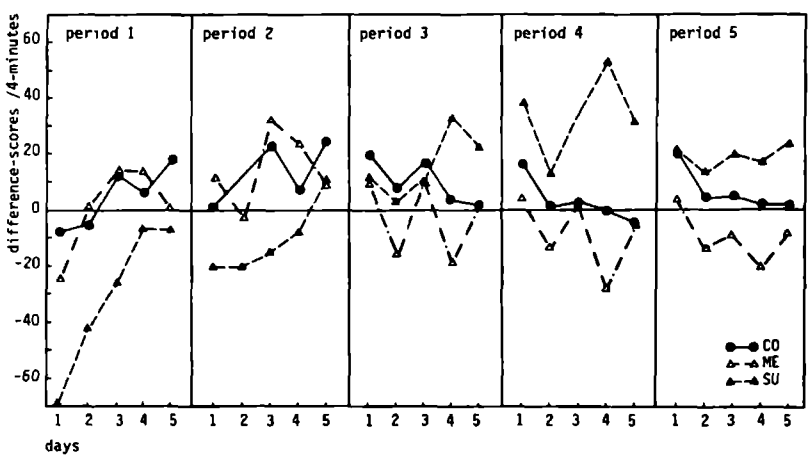

Figure 7.3. Difference-scores obtained in the postsurgery training phase (II), presented per period of 4 minutes. Difference-scores are computed by subtracting each subject's mean scores of the 5 presurgery sessions from each of its corresponding scores of the 5 postsurgery training sessions. Difference-scores are given per day. CO: sham operated control group; SU: group having received sulcal PFC lesions; ME: group having received medial PFC lesions.

Comparison of group ME with the sham controls reveals that, taking the 5 days together, the difference-scores of group ME are significantly lower than those of the controls in period 3 (multiv. $F=4.35$; $df=1,33$; $p<.05$), period 4 (multiv. $F=7.23$; $df=1,33$; $p<.05$) and period 5 (multiv. $F=8.26$;

df=1,33; p<.01). In these three periods group ME responded at a lower level than before surgery. The differences were not large and on the fifth day only those of period 5 still existed. No differences in trends were found for these groups, except for group ME showing more rate oscillations during period 4 (multiv. F=2.87; df=4,30; p<.05).
Comparing group SU with the sham control group (CO) reveals that both groups differ in period 1 (multiv. F=10.27; df=1,33; p<.01), period 2 (multiv. F=6.44; df=1,33; p<.05) and period 4 (multiv. F=7.35; df=1,33; p<.05). In figure 7.3 it can be seen that group SU shows a considerable drop in response rate in the first two periods, when compared with its presurgery level, whereas no such decrease is found for the sham group. The difference in period 4, by contrast, is due to an increase in responding in group SU that is not reflected in the sham controls. Both groups differed in trends only in period 1 (multiv. F=6.71; df=4,30; p<.05), due to the strong linear recovery over days in group SU.
In summary: medial PFC lesions caused a slight decrease in responding in the latter periods of each test session when compared with the sham controls; sulcal PFC lesions resulted in a temporary drop in responding in the first two periods and a higher response rate in period 4.
As it seemed possible that surgery-induced weight losses might account for some of the results, weight loss data were examined. Even though the lesioned groups were given additional food during the first days after surgery, group SU showed larger weight losses than the sham operated group during the entire postoperative test period (p<.01). The mean percentages of weight loss for the groups CO, ME and SU on the first day of testing were 2.9%, 3.1% and 5.2% respectively of the presurgery body weight; on the fifth day of testing amounts of weight loss were .05%, .07% and 3.8% respectively. Group ME did not differ from the control group. However, the differences in weight loss found did not correlate with the response decrements found for group SU (product moment correlations); thus, it seems that they did not influence this drop in responding. Neither have within-group correlations been found between lesion size and the effects considered before (Spearman Rank correlation).

Phase III. Influence of PFC lesions and shifts in reinforcement
Subsequently, 10 sessions were given in which during the third period the regular water reward was replaced by a quinine solution for those subjects assigned to the quinine condition, or by a sucrose solution for those in the sucrose condition. The influences of these changes in the reward upon performance and interactions with the PFC lesions were evaluated again by comparing present scores per period with the presurgery performance. Thus, difference-scores were computed by subtracting each subject's mean of the last 5 presurgery sessions from each of its present scores.
The quinine and sucrose conditions were analyzed separately. Each condition contained the three groups CO, ME and SU, with six subjects each.

1. **Influence of quinine intrusions**
   Figure 7.4 depicts the mean differences in the scores per period (averaged per 2 days) in the groups receiving quinine. Multivariate trend analyses revealed that - taken all groups together - the response rates in the first and second periods had significantly increased relative to presurgery performance (multiv. F=7.68; df=1,15; p<.05 and F=10.90; df=1,15; p<.01). For these two periods no trend effects nor differences between groups were found.
   In the third period response rates decreased considerably, due to the quinine presentation (multiv. F=19.06; df=1,15; p<.01), but again no

trend effects nor differences between groups were found.
In the fourth period all three groups responded at higher levels (multiv. F=14.81; df=1,15; p<.01), which increase became larger over days (multiv. F=4.41; df=9,7; p<.05). Group differences were not observed.
In the fifth period, finally, an increase was apparent also (multiv. F=9.84; df=1.15; p<.01), which in the SU group was larger than in the sham control group (multiv. F=4.43; df=1,15; p<.01). No trend effects were observed.

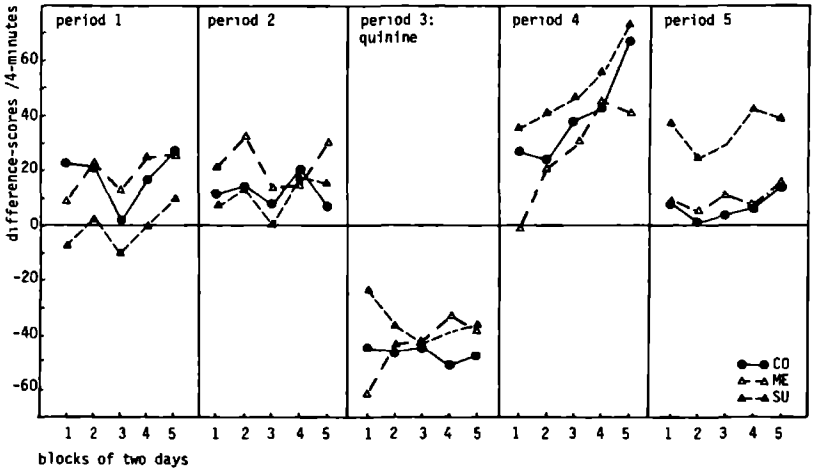

Figure 7.4. Difference-scores obtained during shift sessions are presented per period. Difference-scores are computed by subtracting each subject's mean scores of the 5 presurgery sessions from each of its corresponding shift session scores. Data are averaged per two days. In the third period the water reward was substituted by a quinine solution. Animals were sham operated (CO), or had received a lesion in either the sulcal (SU) or the medial (ME) PFC.

In summary: quinine presentation caused an immediate and permanent drop in responding. During the period following the quinine presentation, in which water was given again, increasingly more responses were made, relative to the presurgery level. Thus, a growing positive contrast effect was demonstrated. In the fifth period the positive contrast effect persisted; it was larger in group SU than in group CO. No other differences between groups were revealed.

2. **Influence of sucrose intrusions**

Figure 7.5 depicts the changes in the scores per period averaged per two days for the groups receiving sucrose. Analyses of the results revealed that - all groups taken together - response rates in the first period were significantly higher than presurgery level (multiv. F=6.54; df=1,15; p<.05). No trend effects nor differences between groups were observed. In the second period no changes were found at all.

In the third period response rates increased considerably (multiv. F=21.47; df=1,15; p<.01), due to the sucrose presentation. Rates kept rising over days (multiv. F=7.16; df=9,7; p<.01); this rise became somewhat less in the latter days of testing. Group differences were absent.
In the fourth period, responding remained at a higher level than prior to surgery (multiv. F=23.66; df=1,15; p<.01), therewith resulting in a positive induction effect. This effect was larger in group SU than in the sham controls (multiv. F=5.23; df=1,15; p<.05). No trend effects were found.
In the fifth period, finally, the increased responding was still apparent (multiv. F=8.56; df=1,15; p<.01), but neither trend effects nor differences between groups were observed.

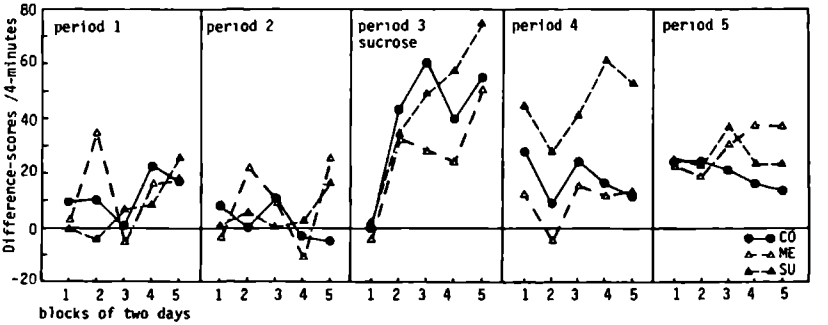

Figure 7.5. Difference-scores obtained during shift sessions are presented per period. Difference-scores are computed by subtracting each subject's mean scores of the 5 presurgery sessions from each of its corresponding shift session scores. Data are averaged per two days. CO: sham operated controls; SU: subjects having received sulcal PFC lesions; ME: subjects having received medial PFC lesions. In the third period the water reward was substituted by a sucrose solution.

In summary: sucrose presentation caused a gradual rise in responding. In both periods following the sucrose presentation a positive induction effect was demonstrated, which in period 4 gradually increased. Only the sulcal group differed from the sham group by showing larger induction effects in period 4. Apart from this, group differences were absent.

7.3.6. Discussion

Phase I. Presurgery retraining
In both Phase I and Phase II response rates within sessions declined considerably. Though in the literature VI schedules are valued particularly for presenting stable response rates (e.g. Nevin, 1973), we systematically found a decline in the course of a 24-min test (see also Chapters IV and V). It seems that with water as a reward response levels are not as stable as suggested.
Apart from this, higher total response scores were produced in this

experiment than in an earlier experiment utilizing the same subjects (Chapter V). These higher response rates are mainly found in the first minutes of each session: 125 responses made in period 1 as compared with 85 responses in the same period in the earlier experiment. In the latter periods of each session, rates were comparable for both experiments: some 30 responses per 4 minutes in period 5. Almost all available rewards were obtained even in the fifth period.

Phase II. Postsurgery training

Prior to the start of Phase II rats had undergone surgery. The main pattern of responding, described above remained unaltered. There were, however, some lesion effects.

1. It was found that medial prefrontal lesions caused a decline in responding for water during the latter periods of each test session. Thus, the pattern of rate decline found prior to surgery was intensified. This accelerated within-session decrease does probably not result from a nonspecific fatigue-like effect, since rats with similar lesions demonstrate normal activity patterns (Sennef, 1985). A comparable decrease in operant responding following medial PFC lesions was also observed with appetitive stimulation of the lateral hypothalamus as the reward (Sennef, 1985). The results seem to be in accordance with reports of reductions in approach tendencies following medial prefrontal lesions (Glass et al., 1969; Gurowitz et al., 1970). Since no lesion effects were found in the shift phase (Phase III) of the experiment in which the incentive value of the reward is explicitly manipulated, the results are probably not caused by a lesion-induced reduction of the incentive value of the reward.
2. Sulcal PFC lesions first of all caused a drop in responding during the initial minutes of the tests; secondly, they caused consistently increased response rates in the latter periods of the tests, particularly so in period 4. The first effect lasted only a few days, whereas the second effect seemed more permanent. The finding that the response reduction was apparent only during the first minutes of the tests and was followed by an enhanced responding in the latter periods, renders an interpretation in terms of an increased drive level less plausible. In connection with the fact that subjects had not been tested for 10 days, it might be suggested that this pause could be responsible for the drop in response rate; presumably, its influence lasted only one day for the medial PFC group and the sham controls. It has been reported that sulcal lesions enhance activity under deprivation conditions (Campbell and Lynch, 1969; Kolb, 1974a) as well as under novel circumstances (De Bruin et al., 1983; Sennef, 1985). This increased activity might initially interfere with efficient barpressing.

The finding that subjects with sulcal PFC lesions maintain this enhanced responding in particularly the third and fourth periods, implies that the within-session decline is retarded. Several interpretations might be considered. First, the behaviour after sulcal lesions might represent a perseveration of high response rates. Perseveration of once-learned predominant behaviours is a frequently observed effect after this type of lesion (Rosvold, 1968; Kolb et al., 1974; Neill, 1976). The drop in responding caused by quinine presentations in Phase III, however, makes this hypothesis less likely correct.

A second interpretation suggests that subjects with sulcal lesions perhaps gain less profit from the rewards and thus need more rewards to reach their prior consumption level; an assumption, then, is that the amount of water consumed contributes to the within-session decline in responding. An

impaired efficiency of consummatory behaviour might be caused by a motor deficit in licking the water from the dipper. Indications for such motor impairments have, however, been found only shortly after surgery (Kolb, 1974a; Brandes and Johnson,1978; Sennef, 1985). However, after longer periods of recovery Kolb (1974b) still observed an increased frequency of eating behaviours, but only during relatively short periods (see also Kolb et al., 1977). This might indicate the occurrence of a more general deficit in adequately switching between consummatory and instrumental behaviours; according to Rice and Campbell (1973) the frontal cortex in connection with the lateral hypothalamus plays a prominent role therein (see also Sennef, 1985).

Phase III. Influence of PFC lesions and shifts in reinforcement

During the shift phase, changing the reward in a more preferred or less preferred direction produced clear rate increases and rate decreases respectively. For quinine an immediate and permanent drop of about 50% was obtained. For sucrose the increase was gradual and resulted in a more than 50% higher response frequency. Both lesions in the prefrontal cortex did not affect these behavioural changes induced by the shifts. That is, the lesioned subjects did adequately respond to changes in the incentive value of rewards.

Following return to the water reward, subjects exposed to quinine showed gradual increases in response rates (up to more than 100% above the preoperative response level); thus, they demonstrated a large positive contrast effect. Subjects having received sucrose during shifts, retained higher response levels after return to the regular water reward, although not as high as during the sucrose presentations; this is must be considered a positive induction effect.

Concerning the influence of PFC lesions on intensity and pattern of development over days of the postshift effects, it appears that medial lesions do not affect these phenomena at all. For the sulcal lesions the results are more complicated. Following quinine presentations, these subjects showed a positive contrast effect that was identical with that of the sham group in the fourth period; in the fifth period, however, they maintained a higher response level than the sham group. Following the sucrose presentations, the sulcal group responded already more than the sham group in the fourth period (i.e. a stronger positive induction effect), whereas in the fifth period no differences between groups were found. Thus, in both cases the sulcal group remained at a higher response level after a period that contained rate increases (i.e. period 4 in the quinine condition and period 3 in the sucrose condition). This might indicate that either the sulcal group persevered at a higher response rate, once it was reached; or the rate increasing effect of the preceding conditions (positive contrast effect and enhanced responding for sucrose respectively) affected their behaviour for a longer time.

An argument against both hypotheses is found in the pattern of development over the 10 days of testing. In the periods in which group SU showed higher response rates than the sham group, the response level was very stable over days, whereas in the preceding periods strong trend effects were consistently found. In our opinion this indicates that both effets, the contrast/induction effects on the one hand and the lesion effects on the other, are independant phenomena.

It might be more plausible to consider the effects of sulcal lesions in the shift phase of the experiment as a continuation of lesion-induced changes already observed in the first postsugery phase (Phase II), which might

result from a less optimal utilization of the rewards obtained. In postsurgery Phase II the effect found was located in the fourth period, as was the effect following sucrose presentation in the shift phase (III). The size of both effects was also comparable. Following the quinine presentation the effect was located in the fifth period, in which during Phase II no effects were found. If we assume that consumption of the quinine solution is less than optimal for all subjects, and that sham and medial groups compensate for this already during the fourth period, it follows that sulcal subjects because of their already mentioned deficits will need more rewards to effectively compensate, and thus will retain increased response levels for a longer period of time.

The results of this experiment strongly suggest that neither the medial nor the sulcal prefrontal cortex are involved in the central processing of the incentive aspects of instrumental conditioning. In contrast, particularly the sulcal PFC seems to play a part in the organization of consummatory behaviour.

Both the contrast effect and the induction effect obtained here were larger than those demonstrated by the same subjects in an earlier experiment (Chapter V). This suggests that either exposing subjects to repeated cycles of the contrast paradigm or prolonged training increases the effects.

Chapter VIII

SUMMARY AND CONCLUSIONS

The initial object of this study has been to investigate the merits of two models explaining the interactions of appetitive and aversive mechanisms in the production of behaviour.

In Chapter I the stage for our studies was set. The identification of approach and avoidance behaviour patterns as crucial for the organism's life, and the subsequent differentiation of appetitive and aversive stimuli respectively as inducing these behaviour patterns have been discussed. The role these stimuli play in learning behaviour has been elaborated as well. Against the background of Hull's nondirectional drive-theory, modern models, based on the appetitive-aversive distinction, were considered. The opponent-process model of Dickinson c.s. postulates two motivational systems, one aversive and the other appetitive. The various stimuli feed into the appropriate system; and each system, once activated, inhibits activity in the other. The opponent-process model of Solomon and Corbit, on the other hand, maintains that each stimulus generates an a-process and -indirectly- also a b-process which opposes the activity of the a-process and thus induces a return to the behavioural equilibrium as existed before the occurrence of the stimulus. Activity of the a-process induces activity of the b-proces. Thus, interactions in this model are assumed to be excitatory rather than inhibitory.

Even though both opponent-process theories considered differ considerably, both imply a symmetry in the appetitive-aversive interactions.

In Chapter II it was argued that experiments employing what is generally known as a contrast paradigm are very well suited to examine this supposed symmetry. The term contrast is used to describe the phenomenon "that exposure to more than one condition of reinforcement exaggerates the difference between the performances maintained by each condition in isolation" (Mackintosh, 1974b). Induction is said to occur when the difference between performances for the two reward values becomes smaller instead. Thus, there is the positive-negative contrast distinction as well as the contrast-induction distinction.

A general review of the contrast literature was given. It was argued that many types of contrast effects can be differentiated and that the various types are not necessarily related. The results within each class of contrast effects are diverse.

From the **successive contrast studies** mainly negative contrast effects have been reported, though in recent times the evidence for positive contrast effects is accumulating also.

The **simultaneous contrast** literature reveals a very commonly found negative contrast effect under a wide variety of conditions, whereas positive contrast effects are found only if certain steps have been taken. The simultaneous positive contrast effect is more difficult to obtain than the successive positive contrast effect. Nevertheless, it can be found and it is found recently by an increasing number of studies. Simultaneous contrast effects are found with many animal species, while the successive contrast effects are observed in rats, but not in pigeons, turtles and fish. This is one of the main reasons why the successive contrast effects might be considered separate from simultaneous contrast phenomena.

The **behavioural contrast** studies are very heavily biased towards positive contrast effects. However, if studies are devised to detect negative

behavioural contrast effects, these are usually found. A special form of contrast, the **local contrast** effect, is found mainly in behavioural contrast studies, though it is not limited to these situations. Both the positive and the negative contrast effect of the local variety are readily demonstrated.
It was concluded that the simultaneous and behavioural contrast effects effects are related phenomena, but that the local and particularly the successive contrast effects are altogether different.
Finally, a short review of the current theoretical concepts explaining contrast effects was given.
In Chapter III the rationale for the specific contrast paradigm chosen in our experiments was elaborated.

Upon summarizing the results of the experiments reported in the next four chapters, it can be concluded that the data fit a definite pattern.
In both experiments described in Chapter IV a positive contrast effect was found and no negative contrast effect after changes in the quality/palatability of the reward. In Chapter V again a positive contrast effect and no negative contrast effect was found following shifts in palatability; no contrast effects were obtained from shifts in the quantity of reward. If reward was omitted entirely during shifts, a very prominent positive contrast effect was revealed. In the experiment reported in Chapter VII, which explored the influence of prefrontal cortex lesions upon this pattern of results, essentially the same was found: after shifts in palatability a positive contrast effect but no negative contrast effect was found. The lesions did not substantially change the general findings. Finally, in the first runway study of Chapter VI, employing water rewards, no contrast effects were found, neither after changes in quality nor after changes in quantityof the reward. When, however, solid food rewards were used, in the second runway study (Chapter VI), a gradually developing positive contrast effect after shifts in palatability, but not after shifts in quantity, was revealed. Also, in both runway studies no indications for negative contrast effects were found.
In summary, positive contrast effects have been repeatedly demonstrated, but again and again no negative contrast effects have been found. The positive contrast effects found have been induced either by shifts in the quality/palatability of the reward or by complete omission of the reward. Size reductions had no such effects.
It has thus been demonstrated that rats readily show positive contrast effects when tested with the procedure commonly employed to produce the effect in pigeons. As with rats the negative contrast effect seems to be the more general phenomenon, these repeated demonstrations of positive contrast effects in the absence of any negative contrast effects are remarkable.
When the results were considered per subject, the same picture arose. Animals exposed to positive contrast conditions showed rather homogeneous response patterns that reflected the general group results. The subjects exposed to negative contrast conditions, on the contrary, showed very variable behaviour, one subject tending to negative contrast effects, another to positive induction effects and yet another showing no behavioural changes at all. This phenomenon appeared in every experiment. On two occasions (see Chapters V and VII) some negative contrast groups tended to positive induction effects. The suggestion that the dishomogeneous response patterns in the negative contrast groups were

related to differences in drive level and/or response level could not be confirmed.

This series of studies has been undertaken with the aim of searching for symmetry in contrast effects, that is, revealing positive as well as negative contrast effects after comparable experimental manipulations. The issue of symmetry must be considered central to the contrast research, as its existence determines the general nature of the theoretical formulations concerning contrast phenomena. If positive and negative contrast effects are essentially symmetrical phenomena, theoretical parsimony is served to the extent that both phenomena are interpreted within the same framework.
Against the background of the general scepticism concerning the existence of positive contrast effects in rats and, consequently, concerning the reality of symmetry also, our repeated demonstrations of positive contrast effects in rats in two different test situations, are indications that positive and negative contrast effects are symmetrical phenomena, at least in some respects. Thus, the choice of palatability/quality of the reward as the shifted parameter has proven correct, as shifting this parameter did produce positive contrast effects in situations where shifting quantity of the reward did not.
However, the fact that in rats the negative contrast effect must be considered a more robust and ubiquitous phenomenon than the positive contrast effect, added to the fact that in our tests we demonstrated a reliable positive but no negative contrast effect after comparable manipulations, indicates that the positive and negative contrast effects are not symmetrical phenomena in all respects.
Procedural details seem largely responsible for the patterns of results obtained. In pigeons positive contast effects have always been common phenomena, whereas negative contrast effects have not been much studied. The dissimilar patterns of results for pigeons as opposed to rats, has often been interpreted as the result of differences in response topographies. For pigeons, the keypeck response required closely resembles the consummatory response (eating) that is performed once the reward is obtained. In contrast, the barpress response required from rats seems further removed from this final consummatory response. However, these differences in response topographies cannot account for the general discrepancy in the results obtained with rats and pigeons. First, the argument holds only if rats invariably press the lever with their paws. Observations of rats in operant chambers has revealed that this need not be so. Many rats vigorously gnaw and bite at the lever and activate it that way. A large degree of individual variation was observed, as well as many rats switching from one strategy to the other. Nevertheless, many rats, indeed, predominantly used their paws. Secondly, even though most rats used their paws, we reliably demonstrated positive contrast effects. Since the positive contrast groups demonstrated very homogeneous response patterns, irrespective of the way they activated the lever, this clearly speaks against the response topography argument.
The fact that positive contrast effects with rats occur more reliably under delayed as compared to immediate reward conditions, suggests the operation of a ceiling effect which precludes the increase of performance levels and hence of positive contrast. The problem of a ceiling effect arises when animals perform at such high levels that they are near their physical limits and cannot improve (overshoot) even further. This argument often seems to hold, at least in runway situations, which are the test situations most commonly used with rats. In leverpress situations the danger of

ceiling effects can be avoided by adapting the schedule requirements. In the experiments described in Chapter IV, V and VII, which employed a leverpress response, there was no question of ceiling effects. In the runway tests described in Chapter VI they might have played a part, as -notwithstanding the turns and hurdles- our rats were running very fast. In the first runway study reported, indeed, no positive contrast effects were obtained and it might have been attributable to the operation of a ceiling effect, were it not that in our second runway study subjects ran even faster and yet the group exposed to quinine adulterated food rewards developed a positive contrast effect. Why no positive contrast effects were observed in the first runway experiment remains unclear. Our conclusion therefore is that, if the occurrence of ceiling effects has been eliminated one way or another, rats can and do show positive contrast efects. Thus, evaluated against the contrast literature, our repeated demonstrations of positive contrast effects cannot be considered just chance findings.

Since the negative contrast effect in rats is usually easily found, there has never been a need to invoke the pendant of the ceiling effect, the floor effect, as an explanation for a lacking negative contrast effect. A floor effect may operate when response levels drop so low that undershooting that level is no more possible. In our first leverpress study (Chapter IV) a floor effect might have prevented the occurrence of a negative contrast effect following the second shift, as indeed response rates in the 6th and 7th periods of the tests were already quite low before rewards were manipulated. However, the absence of a negative contrast effect after the first shift can not be attributed to a floor effect, as in period 3 and 4 response levels were definitely high enough to allow a considerable undershooting. Moreover, in the subsequent studies, reported in Chapter V and VII, the experimental procedure was adapted to circumvent the danger of a floor effect; even so, no negative contrast effects were found. Finally, in the runway studies, where there was hardly any opportunity for floor effects to influence performance, no negative contrast effects were found either.

The fact that we were unable to produce the generally reliable negative contrast effects under conditions similar to those that did produce positive contrast effects, indicates that even though the positive and negative contrast effects both are reliable phenomena, they are not symmetrical in all respects.

Our search for symmetry was motivated by the two theories on appetitive aversive interactions discussed in Chapter I. Dickinson and Dearing (1979) explicitly assume that the organization of the appetitive mechanism is essentially identical with that of the aversive system, stimuli of a particular affective value activating the matching system, which inhibits the opposite system. Solomon and Corbit (1974) imply that the standard pattern of a primary reaction followed by an after-reaction is found whether the primary reaction was pleasurable or aversive. Thus, departing from both these theories, symmetry was to be expected.

As in all our studies negative contrast effects were entirely absent, this hypothesis of symmetry in appetitive-aversive interactions does not fare well. It must be remembered (see 1.3) that the evidence for symmetry from Pavlovian conditioning studies, as reviewed by Dickinson and Pearce (1977) and Dickinson and Dearing (1979), is not conclusive either: aversive stimuli inhibit appetitive behaviour, but the reverse is less consistently found; appetitive inhibitors modulate aversive conditioning, but there is

little evidence that an aversive inhibitor affects appetitive conditioning.

Other assumptions of both models encounter difficulties also. The most striking departure from the predictions is found in our data indicating that clear shift effects did not necessarily generate subsequent contrast effects, and conversely, that the absence of shift effects did not preclude the occurrence of contrast effects. For example, in Chapter IV, the second experiment, group SW demonstrated no shift effect but a clear positive contrast effect, whereas the shift effect of group WS was not followed by a contrast effect. These data do not fit the rebound assumption of inhibitory interaction models, which suggests that shift effects and contrast effects are proportional in size. Neither do they follow Solomon and Corbit's prediction that with repeated exposures to affective stimuli (shifts) the primary effect (shift effect) should diminish in size, whereas the secondary effect (contrast effect) should become larger (See Chapter I, Figure 1.5). No consistent indications were found that over days shift and/or contrast effects changed in size; sometimes they did and sometimes they did not.

In conclusion, since it seems highly likely that methodological detail has had an impact on the results of our studies, as it has on the research into contrast effects in general, our studies cannot be considered conclusive evidence either in favour of or against the existence of symmetry. As it is, the positive and negative contrast effects seem differently sensitive to various procedural manipulations. Since neither of the above-mentioned opponent-process models allows for such differences, they can not explain the various patterns of contrast effects obtained. Thus, the conflicting results from our studies as well as from the general field of contrast research challenge both theories on several grounds. Unless some adaptations have been made to allow for these findings, both theories must be considered inadequate, at least as a model for contrast effects.

SAMENVATTING EN CONCLUSIES

De bestudering van het gedrag van vele diersoorten heeft duidelijk aangetoond dat gedrag is georganiseerd rond enerzijds het nastreven van biologisch belangrijke prikkels of stimuli, die te maken hebben met het levensonderhoud, en anderzijds de vermijding van schadelijke of bedreigende prikkels. Deze stimuli noemt men ook wel affectieve of incentieve stimuli; een stimulus die het dier opzoekt, noemt men appetitief; een stimulus die het vermijdt, noemt men aversief. Deze affectieve stimuli die het gedrag dus een verschillende richting geven, hebben ook verschillende effecten in een leerproces. Een appetitieve stimulus werkt als beloning (reward) die het beloonde gedrag in frequentie doet toenemen; een aversieve stimulus werkt als straf (punishment) die het betreffende gedrag doet afnemen. Beloningen en straf vat men samen onder de term reinforcers en het effect van deze stimuli op het ontstaan van prikkel-respons associaties -de basis van het leren- noemt men reinforcement.
Niet alleen het optreden van de stimulus, maar ook de beeindiging ervan kan affectieve invloed hebben en dus met succes als beloning of straf worden benut. Wat hierbij opvalt, is dat de reactie van het dier op de beeindiging van een stimulus affectief tegengesteld is aan die op de introductie van de stimulus. Zo is shock aversief en leidt tot vermijdings- of ontsnappingsgedrag; het ophouden van shock veroorzaakt een soort opluchting. Het krijgen van voer roept een toenaderingsgedrag op; het achterwege blijven van voer dat wordt verwacht, roept frustratie op. Men spreekt dan ook van "reward" versus "frustrative nonreward" en van "punishment" versus "relief of punishment". De effecten van het beeindigen van de beloning cq. straf op het leergedrag zijn ook tegengesteld aan die van het aanbieden van de betreffende affectieve stimulus.

Bij de theorievorming omtrent de mechanismen die het gedrag ten aanzien van appetitieve en aversieve stimuli realiseren, wordt tegenwoordig gewoonlijk aangenomen dat er op centraal/neuraal niveau twee motivatie-systemen bestaan, een appetitief en een aversief systeem. De verschillende incentieve stimuli worden in deze systemen verwerkt: ze genereren in samenspel met de bijbehorende motivationele toestanden ofwel appetitieve ofwel aversieve reacties. Het element van dualiteit, dat kenmerkend is voor de recente motivatie-theorieen, blijkt dus niet alleen op het niveau van de gehanteerde begrippen, maar ook op het niveau van de eraan ten grondslag gedachte neurale strukturen en processen.
In het algemeen neemt men aan dat de mate van toenaderings- of vermijdings gedrag bepaald wordt door de relatieve activiteit van beide motivationele systemen. Daarbij zijn de centrale appetitieve en aversieve mechanismen niet onafhankelijk van elkaar. Men is het er algemeen over eens dat ze qua werking aan elkaar tegengesteld zijn, en dat ze elkaar bovendien tegenwerken. Dat deze twee systemen elkaar beinvloeden, blijkt met name uit het bovengenoemde feit dat beeindiging van een stimulus een reactie tot gevolg heeft die tegengesteld is aan die op introductie van de stimulus. Hoe evenwel deze interacties worden gerealiseerd, is onderwerp van veel speculatie.

Het doel van de in dit proefschrift beschreven studies is geweest de verdiensten te bekijken van twee modellen die de appetitieve-aversieve interacties in de productie van het uiteindelijke gedrag proberen te verklaren. Deze modellen zijn in Hoofdstuk I nader uitgewerkt.

Aan de ene kant is er het excitatoire interactie-model van Solomon en Corbit (1974). Dit model gaat er van uit dat het organisme streeft naar een affectief evenwicht, vergelijkbaar met het idee van homeostase in de fysiologie. Om dit evenwicht te bereiken moet elke stimulus die leidt tot een affectieve evenwichtsverstoring worden tegengewerkt. Solomon en Corbit nemen daartoe aan dat elke prikkel eerst een a-proces genereert en daarna, indirect, via het a-proces, een b-proces in gang zet dat de activiteit van het primaire a-proces remt en daardoor een terugkeer naar een gedragsevenwicht bewerkt. Als het primaire a-proces niet meer actief is omdat de stimulatie ervan is beeindigd, wordt ook de excitatie van het b-proces beeindigd. Het b-proces heeft echter, in tegenstelling tot het a-proces, een lange uitloopperiode. Dit verschil in tijdsverloop nu veroorzaakt een tijdelijk op de voorgrond treden van het secundaire b-proces, resulterend in het optreden van een na-effect van de stimulus dat tegengesteld is aan het primaire effect.
Lijnrecht hier tegenover staat het inhibitoire interactie-model van Dickinson c.s. (bijv. Dickinson en Dearing, 1979). Dit model veronderstelt dat er twee motivatie-systemen zijn, een appetitief en een aversief. De appetitieve en aversieve prikkels worden elk alleen in het bijbehorende systeem verwerkt: de appetitieve in het appetitieve motivatie systeem en de aversieve in het aversieve motivatie systeem. Zodra een van de systemen tot activiteit is gebracht, remt het de activiteit in het andere. Omdat men aanneemt dat de mate van appetitief en aversief gedrag bepaald wordt door de relatieve activiteit van beide systemen, resulteert hieruit de assumptie dat toename in appetitieve stimulatie equivalent is aan afname van aversieve stimulatie en vice versa. Anders gezegd, "punishment" en "nonreward" zijn equivalent, "reward" en "relief of punishment" eveneens. De na-effecten die men ziet na beeidiging van de stimulus worden in dit model nauwelijks bestudeerd, ofwel impliciet gezien als resultaat van een opheffing van de inhibitie van het door de stimulus geremde systeem en een "rebound" naar een niveau dat tijdelijk hoger ligt dan normaal.
Hoezeer deze modellen ook van elkaar verschillen, beide impliceren dat de appetitieve-aversieve interacties symmetrisch zijn.

In Hoofdstuk II wordt uiteen gezet dat experimenten die gebruik maken van wat gemeenlijk het contrast paradigma wordt genoemd, buitengewoon geschikt zijn om na te gaan of deze symmetrie te vinden is. Hoewel de contrast literatuur tot op heden nauwelijks betrokken wordt bij de theorievorming omtrent excitatoire en inhibitoire interactie-modellen van de affectieve dynamica, lijkt ze bij uitstek relevant. In een contrast procedure namelijk worden de effecten van het aanbieden van een stimulus -de beloning of ermee geassocieerde stimuli- vergeleken met de na-effecten die optreden na beeindiging ervan. Ook hier is het al dan niet symmetrisch zijn van de effecten van theoretisch belang.
In een contrast procedure leert het proefdier om met een relatief constant tempo een bepaald gedrag uit te voeren (het basis respons niveau). Voor dit gedrag krijgt het dier een bepaalde beloning. Vervolgens worden kortdurende veranderingen in bijvoorbeeld de kwaliteit, de kwantiteit of de waarschijnlijkheid van de beloning aangebracht; dit noemt men een "shift". De prestaties van het dier veranderen overeenkomstig de richting van de verschuiving in de beloning: wordt de beloning slechter, dan ziet men een daling, wordt ze beter, dan ziet men een stijging in het respons niveau (shift effect). Na enige tijd wordt dan weer de oorspronkelijke beloning aangeboden. Van een contrast effect is sprake als na een verschuiving die

een verslechtering van de beloning inhield, de oorspronkelijke beloning positiever wordt gewaardeerd dan voorheen (tot uitdrukking komend in een verhoogd respons niveau), of wanneer na een verschuiving in positieve richting de oorspronkelijke beloning lager wordt gewaardeerd (verlaagd respons niveau). Wanneer het respons niveau behorend bij een bepaalde waarde van de beloning toeneemt ten gevolge van de voorafgaande presentatie van een beloning van geringere waarde, spreekt men van een positief contrast effect; het omgekeerde noemt men een negatief contrast effect. Als het respons niveau ten gevolge van de voorafgaande presentatie van een beloning met geringere waarde verlaagd blijft, spreekt men van negatieve inductie; de tegenhanger hiervan is positieve inductie.
Men onderscheidt dus enerzijds positieve en negatieve contrast effecten, anderzijds positieve en negatieve inductie effecten.
In Hoofdstuk II wordt vervolgens een algemeen overzicht gegeven van de contrast literatuur. Geconcludeerd wordt dat er vele typen van contrast zijn te onderscheiden, die niet noodzakelijk aan elkaar verwant zijn.
In onderzoekingen met betrekking tot het successieve contrast worden voornamelijk negatieve contrast effecten gevonden, hoewel de laatste tijd het aantal studies dat er in slaagt ook positieve contrast effecten aan te tonen, toeneemt.
Uit de literatuur aangaande simultaan contrast kan worden geconcludeerd dat het negatieve contrast effect een zeer algemeen fenomeen is dat onder de meest uiteenlopende omstandigheden wordt gevonden. Het positieve contrast effect daarentegen is moeilijker te vinden. Niettemin, als men op bepaalde voorwaarden goed acht slaat, kan het worden aangetoond. Het wordt de laatste tijd dan ook steeds vaker gevonden. Simultane contrast effecten worden in vele diersoorten gevonden, terwijl successieve contrast effecten alleen zijn aangetoond in ratten, maar niet in duiven, schildpadden en vissen. Op grond daarvan neemt men aan dat de successieve contrast effecten nagenoeg niet verwant zijn aan de simultane contrast effecten.
"Behavioural" contrast studies hebben zich traditioneel voornamelijk bezig gehouden met de bestudering van positieve contrast effecten en gebruikten bij voorkeur duiven als proefdier. Studies die beoogden ook negatieve contrast effecten aan te tonen, slaagden daar meestal ook in.
Een speciale vorm van contrast is het locale contrast effect dat alleen optreedt onmiddellijk na de overgang van de ene beloning (of de ermee geassocieerde stimulus) naar de andere. Het locale contrast wordt meestal gevonden binnen "behavioural" contrast studies, hoewel het daartoe niet beperkt is. Zowel het negatieve als het positieve locale contrast effect worden regelmatig gevonden.
Simultane en "behavioural" contrast effecten lijken verwante fenomenen te zijn; de locale contrast effecten en met name de successieve contrast effecten staan er grotendeels los van..
Tenslotte wordt in Hoofdstuk II een overzicht gegeven van de belangrijkste theoretische concepten die de contrast effecten pogen te verklaren.

In Hoofdstuk III wordt uiteengezet op welke gronden in de volgende experimenten voor het contrast paradigma is gekozen, en met name voor bepaalde wijzigingen en variaties daarin.
In Hoofdstuk IV en V worden experimenten beschreven waarin ratten getraind worden om op een hefboom te drukken voor een water beloning. Nadat ze dit geleerd hebben, wordt gedurende korte periodes in een sessie de beloning gewijzigd; ofwel de kwaliteit -in ons geval de smaak- wordt veranderd door toevoeging van kinine (negatief) dan wel suiker (positief); ofwel de hoeveelheid wordt verminderd (negatief) dan wel vermeerderd (positief). In

het aantal malen dat op de hefboom wordt gedrukt, komt de waardering voor de beloning tot uitdrukking.
In Hoofdstuk VI worden twee experimenten beschreven waarin ratten getraind worden om door een loopgang te rennen om aan het einde daarvan een beloning te vinden die in het ene experiment uit water, in het andere uit voer bestaat. De dieren lopen 16 keer per dag; gedurende een drietal beurten wordt de beloning gewijzigd, ofwel wat de kwaliteit betreft, door toevoeging van suiker of kinine, ofwel wat de hoeveelheid betreft, meer of minder dan tevoren of erna. Uit de loopsnelheid van de dieren wordt de waardering voor de beloning afgeleid.
In Hoofdstuk VII tenslotte wordt een experiment gerapporteerd waarin de dieren weer leren op een hefboom te drukken voor water. Wanneer ze dit gedrag geleerd hebben, wordt de prefrontale cortex, een gedeelte van de hersenen dat betrokken lijkt bij de organisatie van appetitief en aversief gedrag, vernietigd, en worden de dieren blootgesteld aan de contrast procedure uit Hoofdstuk V.

Wanneer men de resultaten van de experimenten die worden gerapporteerd, overziet, valt op dat de data een zeker patroon vormen. In de beide experimenten uit Hoofdstuk IV wordt wel een positief contrast effect maar geen negatief contrast effect gevonden na veranderingen in de kwaliteit (smaak) van de beloning. In Hoofdstuk V wordt opnieuw een positief contrast effect en geen negatief contrast effect gerapporteerd na veranderingen in smaak, en helemaal geen effect na verandering in de hoeveelheid van de beloning. Wanneer evenwel de beloning geheel wordt weg gelaten, wordt daarna een zeer aanzienlijk positief contrast effect gevonden. In Hoofdstuk VII, dat de invloed van lesies in de prefrontale cortex op dit patroon van resultaten beschrijft, wordt in feite het zelfde gevonden: veranderingen in de smaak van de beloning veroorzaken een positief maar geen negatief contrast effect. De lesies hebben geen noemenswaardige invloed hierop. Tenslotte wordt in de eerste loopgang studie van Hoofdstuk VI, waarin de beloning bestaat uit water, geen enkel contrast effect gevonden, noch na wijzigingen in de kwaliteit/smaak, noch na wijzigingen in de hoeveelheid van de beloning. Wanneer de beloning bestaat uit voer, zoals in het tweede experiment uit dit hoofdstuk, wordt wel een zich geleidelijk ontwikkelend positief contrast gevonden na verandering in smaak, maar niet na verandering in hoeveelheid. Ook in beide loopgang studies worden geen aanwijzingen gevonden voor negatieve contrast effecten.
Samengevat: Positieve contrast effecten werden herhaaldelijk gevonden, maar negatieve contrast effecten in geen enkel experiment. De positieve contrast effecten werden geinduceerd door ofwel veranderingen in de kwaliteit (smaak) ofwel een geheel weglaten van de beloning tijdens de shift. Vermindering van de beloning leidde daarentegen niet tot een positief contrast effect.
Hiermee werd aangetoond dat men bij ratten gemakkelijk een positief contrast effect kan vinden, wanneer men deze dieren test in de situatie die gewoonlijk gebruikt wordt om een positief contrast te produceren bij duiven. Daarentegen werden geen negatieve contrast effecten gevonden. Aangezien bij ratten het negatief contrast effect een veel algemener fenomeen is dan het positief contrast effect, is deze herhaalde demonstratie van een positief contrast effect bij een ontbreken van een negatief contrast effect een opmerkelijk resultaat.
Wanneer men de resultaten per rat bekijkt, ziet men ongeveer hetzelfde. De dieren uit positief contrast condities toonden een tamelijk homogeen

respons patroon dat de algemene resultaten weerspiegelt. De dieren uit de negatief contrast condities echter gedroegen zich vaak zeer verschillend na de verandering in de beloning: de een neigde naar negatief contrast, de ander naar positieve inductie en weer een ander toonde geen enkele verandering. Dit werd in elk experiment gevonden.

De serie experimenten werd uitgevoerd met het doel symmetrie in het optreden van contrast effecten te vinden, d.w.z. positieve zowel als negatieve contrast effecten aan te tonen na vergelijkbare experimentele manipulaties. Het vraagstuk van de symmetrie is een essentieel aspect van onderzoek naar contrast verschijnselen. Immers, de al dan niet aanwezigheid ervan is in hoge mate bepalend voor de aard van de theoretische formuleringen met betrekking tot contrast effecten. Als positieve en negatieve contrast effecten symmetrische verschijnselen zijn, zou het theoretisch wenselijk zijn dat beide verschijnselen ook binnen hetzelfde kader worden geinterpreteerd.
Tegen de achtergrond van de algemene skepsis ten aanzien van het bestaan van positief contrast in ratten en, dientengevolge, ten aanzien van de realiteit van symmetrie, vormt onze herhaalde demonstratie van positieve contrast effecten in ratten in twee verschillende test-situaties, een aanwijzing dat positieve en negatieve contrast effecten symmetrische fenomenen zijn, op zijn minst in bepaalde opzichten. Het feit evenwel dat in ratten het negatieve contrast effect een veel robuuster en algemener fenomeen is dan het positieve contrast effect, gevoegd bij het feit dat wij er niet in slaagden een negatief contrast effect aan te tonen onder dezelfde condities die wel een positief contrast effect induceerden, wijst erop dat positieve en negatieve contrast effecten niet in alle opzichten symmetrisch zijn.
Procedurele details lijken voor een groot deel verantwoordelijk voor het patroon van verkregen resultaten. In duiven zijn positieve contrast effecten altijd veel gevonden effecten geweest, terwijl negatieve contrast effecten weinig werden onderzocht. Het verschil in resultaten verkregen met duiven of ratten wordt wel toegeschreven aan verschillen in de respons die van duiven en ratten wordt gevraagd. De pikrespons die duiven meestal moeten maken, is zeer nauw verwant aan de consummatoire respons (eten) die wordt uitgevoerd zodra de beloning is verkregen. Het drukken op een hefboom, de respons die van ratten wordt gevraagd, staat daarentegen veel verder af van die consummatoire eindrespons. Niettemin kunnen deze verschillen het uiteenlopende patroon van resultaten bij duiven en rattten niet verklaren. Ten eerste, het argument geldt immers alleen indien ratten de hefboom uitsluitend met hun poten bedienen. Dit nu is niet het geval: vaak bijten ze in de hefboom en zetten deze zo in werking. Veel ratten wisselen ook voortdurend van strategie. Ten tweede, ondanks het feit dat veel ratten inderdaad vooral hun poten gebruikten, toonden wij betrouwbare positieve contrast effecten aan. Aangezien de positieve contrast groepen zeer homogene respons-patronen lieten zien, ongeacht of ze de hefboom met poten en/of bek activeerden, is dit een duidelijk argument tegen de hypothese die is gebaseerd op verschillen in respons-topografie.
Het feit dat positieve contrast effecten bij ratten eerder worden gevonden wanneer de verdiende beloning niet onmiddellijk wordt gegeven maar kort wordt uitgesteld, suggereert dat een plafond effect vaak het optreden van positieve contrast effecten verhindert. Een plafond effect ontstaat zodra de dieren op een zo hoog niveau presteren dat ze dicht bij de grenzen van wat fysiek mogelijk is komen, m.a.w. niet nog beter kunnen presteren. Dit argument snijdt met name hout in testsituaties waarin loopsnelheid wordt

gemeten, dus precies in die situatie waarin ratten het vaakst worden getest. In de experimenten beschreven in Hoofdstuk VI zouden plafond effecten een rol hebben kunnen spelen, daar de dieren zeer hard liepen. Het ontbreken van een positief contrast effect zou zo verklaard kunnen worden, ware het niet dat in het tweede experiment de dieren zo mogelijk nog harder liepen en de groep die was blootgesteld aan kinine desalniettemin geleidelijk een positief contrast effect ontwikkelde. Waarom in het eerste experiment geen positief contrast effect werd gevonden, blijft vooralsnog onduidelijk.
Onze conclusie is dan ook dat, zodra interferentie door plafond effecten is voorkomen, ratten zeer goed in staat zijn positieve contrast effecten te vertonen en dat inderdaad ook doen. In het licht van de omvangrijke contrast literatuur kunnen onze herhaalde demonstraties van positief contrast in ratten dan ook niet beschouwd worden als toevalstreffers.
Aangezien het negatieve contrast effect bij ratten gewoonlijk gemakkelijk gevonden wordt, is er nooit enige noodzaak geweest de tegenhanger van het plafond effect, het bodem effect, voor te stellen als een verklaring voor het ontbreken van negatieve contrast effecten. Een bodem effect is aanwezig zodra de prestaties van de dieren zo laag liggen dat ze bijna niet nog lager kunnen. In het eerste experiment waar ratten op een hefboom drukten (Hoofdstuk IV) was dit gevaar zeer groot: met name in de laatste periodes van elke testsessie respondeerden de dieren zeer weinig. Dat verklaart echter niet waarom in de eerdere periodes geen negatieve contrast effecten werden gevonden. In de volgende experimenten (Hoofdstuk V en VII) werd het gevaar van een bodem effect ondervangen; niettemin werden geen negatieve contrast effecten gevonden. Ook in de loopgang-experimenten (Hoofdstuk VI) waar bodem effecten nauwelijks een probleem vormen, werden geen negatieve contrast effecten gevonden.
Het feit dat wij er niet in slaagden negatieve contrast effecten te demonstreren onder omstandigheden waaronder we het positieve contrast effect wel aantoonden, wijst er op dat, hoewel de positieve en negatieve contrast effecten beide betrouwbare fenomenen zijn, ze niet in alle opzichten symmetrisch zijn.

Ons uitgangspunt in dit onderzoek naar symmetrie werd gevormd door de twee theorien aangaande appetitieve-aversieve interacties, die werden besproken in Hoofdstuk I. Dickinson en Dearing (1979) stellen expliciet dat de organisatie van het appetitieve mechanisme fundamenteel identiek is aan die van het aversieve systeem; stimuli van een bepaalde affectieve waarde activeren dus het bijbehorende systeem en inhiberen het tegengestelde systeem. Solomon en Corbit (1974) impliceren dat het standaard reactie-patroon, bestaande uit een primaire reactie gevolgd door een na-effect, gevonden wordt ongeacht de aard, aversief of aangenaam, van de primaire reactie. Dus, op basis van beide theorien zou men symmetrie verwachten. Door het ontbreken van negatieve contrast effecten in al onze studies komen beide theorien in moeilijkheden. De evidentie die Dickinson c.s. bespreken ter ondersteuning van hun model en die voornamelijk afkomstig is uit studies naar klassiek conditioneren, is evenmin erg overtuigend in dit opzicht.
Andere assumpties van beide modellen komen er evenmin erg goed af. De meest opvallende afwijking van de predicties is wel de bevinding dat duidelijke shift effecten niet noodzakelijkerwijs leiden tot contrast effecten, en omgekeerd, dat het ontbreken van shift effecten het optreden van contrast effecten in het geheel niet uitsluit. Deze data passen niet in de "rebound" assumpties van inhibitoire interactie-modellen, die

suggereren dat shift effecten en contrast effecten proportioneel in omvang zouden moeten zijn. De data passen echter evenmin in de voorspelling van Solomon en Corbit dat met herhaalde aanbieding van affectieve stimuli de primaire reactie (hier het shift effect) kleiner , het na-effect (hier het contrast effect) daarentegen groter zou moeten worden (Zie Hoofdstuk I, Figuur 1.5). Wij vonden geen consistente aanwijzingen voor systematische veranderingen over dagen.

Wij zouden het volgende willen concluderen. Aangezien het zeer waarschijnlijk is dat methodologische details van invloed zijn geweest op onze resultaten, zoals ook op het onderzoek naar contrast effecten in het algemeen, kunnen onze resultaten niet beschouwd worden als uitsluitsel gevende evidentie voor of tegen het bestaan van symmetrie in contrast verschijnselen. Het is waarschijnlijk dat positieve en negatieve contrast effecten in verschillende mate gevoelig zijn voor allerlei procedurele manipulaties. Aangezien geen van beide genoemde "opponent-process" theorien rekening houdt met zulke verschillen, zijn ze niet in staat de verkregen resultaten te verklaren. De data van onze studies, evenals van het contrast onderzoek in het algemeen, vormen een uitdaging voor beide theorien. Zolang deze theorien niet op een aantal punten zijn bijgesteld, moeten beide, in elk geval als model voor contrast verschijnselen, als inadequaat worden beschouwd.

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DANKWOORD

Dit proefschrift is gebaseerd op een reeks experimenten die zijn uitgevoerd bij de Vakgroep Vergelijkende & Fysiologische Psychologie van het Psychologisch Laboratorium van de KUN.
Ik ben zeer erkentelijk voor de prettige sfeer binnen deze vakgroep en de genoten vriendschap. Zonder de daadwerkelijke bijstand van een aantal medewerkers had ik dit onderzoek en proefschrift niet kunnen voltooien.
Veel dank ben ik verschuldigd aan Ben ten Tusscher, Agnes Oomen en Chris Poirot, die als student cq. studentenassistent mij behulpzaam zijn geweest bij delen van dit onderzoek.
Zonder de enthousiaste medewerking van Thijs Janssen die een deel van de dieren heeft getraind, waren de runway-proeven onuitvoerbaar geweest. Het snelheidsrecord staat op naam van een van zijn ratten. Thijs en Hans Krijnen dank ik eveneens voor de zorgvuldige wijze waarop zij altijd voor mijn proefdieren hebben gezorgd.
Tevens voel ik mij ten zeerste verplicht aan de afdeling Electronica, die in het prille begin van de automatisering van de Skinnerboxen-opstelling menige onverwachte storing en geheimzinnige kinderziekte heeft moeten verhelpen. Speciaal dank ik ook Marty Wansink die, toen een deel van het manuscript verloren dreigde te gaan door een storing in de computer, een en ander heeft weten te redden, en daarna de computer repareerde met alcohol en zakdoek.
Zeer veel dank ben ik ook verschuldigd aan John van Betteray voor de uiterst nauwkeurige wijze waarop hij het manuscript heeft nageplozen en van fouten en inconsequenties heeft ontdaan.
De tekeningen zijn vervaardigd door Dorette Gerrits en het manuscript is geprint met medewerking van Chris Bouwhuisen. Beiden wil ik hartelijk danken. Ook Bennie Hoefnagel, die dit proefschrift in sneltreintempo heeft gedrukt, mag niet onvermeld blijven.
Alle genoemde en niet genoemde personen die op enigerlei wijze hebben bijgedragen aan en/of meegeleefd met de tot stand koming van dit proefschrift ben ik zeer erkentelijk.
En tenslotte, zeer veel dank ook aan mijn ouders en Fons en Lino, die dit proefschrift hebben mogelijk gemaakt, en aan Miriam die altijd al gedacht had dat het wel lukken zou.

CURRICULUM VITAE

Hanneke Receveur werd op 4 juli 1944 geboren te Steyl.
Van 1956 tot 1962 bezocht ze het gymnasium "St. Angela", Jeruzalem, te Venray, alwaar ze in 1962 het diploma gymnasium α behaalde.
Na van 1962 tot 1964 Sociale Geografie te hebben gestudeerd, studeerde ze van 1965 tot 1974 psychologie aan de Katholieke Universiteit te Nijmegen. Haar hoofdrichting was Vergelijkende & Fysiologische Psychologie; eerste uitbreiding was Psychologische Funktieleer, en de bijvakken waren Neurofysiologie en Botanie. Op 22 juni 1974 legde zij het doktoraal examen, cum laude, af.
Na een verblijf van een jaar in Nieuw Zeeland, volgde eind 1975 de aanstelling als junior medewerker aan de Vakgroep Vergelijkende & Fysiologische Psychologie aan de KUN. Op een tijdelijke onderzoeksplaats -projekt SW1/75 van de universitaire onderzoekspool- werd onderzoek verricht naar neurale reactie-mechanismen bij herhaald aangeboden stimuli. In eerste instantie werd dit onderzoek gericht op gedragsveranderingen ten gevolge van temperatuur-stimulatie, intracraniele stimulatie en milde electroshocks. In het tweede gedeelte van dit projekt werd uitvoering gegeven aan het in dit proefschrift beschreven onderzoek naar de symmetrie van appetitieve-aversieve interacties, met gebruik making van het contrast paradigma.

STELLINGEN

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1. Het gegeven dat bij duiven overwegend positieve contrast effecten worden gevonden en bij ratten voornamelijk negatieve, kan niet verklaard worden vanuit tussen beide diersoorten bestaande verschillen in topografie van de vereiste respons.

2. De evolutie van mechanismen zoals die in contrast verschijnselen manifest worden, stelt het organisme in staat om de gevolgen van handelingen te relateren aan verwachtingen omtrent deze gevolgen en maakt daarmee een correctie van handelen mogelijk.

3. Het bij herhaling geconstateerde feit dat VI-schema's van reinforcement niet tot een over langere tijd constant blijvende 'baseline' van responderen leiden, doet twijfels rijzen met betrekking tot de stabiliteit van de VI-schedule 'baselines' zoals vermeld in de literatuur.

4. Het verdient aanbeveling om in dierexperimenteel onderzoek waar water/voer als beloning wordt gebruikt, de dieren niet onmiddellijk na afloop van de gedragstests hun dagelijkse rantsoen te verstrekken.

5. Wanneer wetenschappers de universiteit verlaten in een heilig geloof in de wetenschap en de wetenschappelijke methode, heeft de universitaire opleiding gefaald in het hen bijbrengen van methodische twijfel en kritische zin.

6. Het is onjuist uit het feit dat dieren onze bedoelingen vaak niet begrijpen, te concluderen dat mensen intelligenter zijn.

7. Ten onrechte worden massale strandingen van walvissen in de pers nog altijd beschreven als een vorm van zelfmoord.

8. Wanneer vossen bejaagd worden uit het oogpunt van volksgezondheid, is het middel erger dan de kwaal.

9. Begrazing van onze natuurgebieden door zogenaamde primitieve huisdierrassen en andere grote grazers, is een fraaie vorm van modern natuurbeheer, mits men zich ook verdiept in en rekening houdt met de behoeften, leefwijzen en gewoonten van de ingezette dieren.

10. Historisch onderzoek naar het bestaan van de van telgang afgeleide laterale gangen bij rijpaarden enerzijds, en naar de omvang van het gebruik van die gangen anderzijds, wordt ernstig gehinderd door de meestal niet ter zake deskundige vertalingen van klassieke en middeleeuwse bronnen. Het daaruit voortvloeiende onjuiste gebruik van de desbetreffende terminologie is er bovendien de directe oorzaak van dat deze gangen momenteel vrij algemeen als niet-natuurlijk worden beschouwd.

11. Wie van oordeel is dat men om goed paardrijden te leren er een aantal keren dient af te vallen, miskent dat het de essentie van paardrijden is om boven te blijven.

Nijmegen, 14 maart 1985 Hanneke Receveur.